SPECIES DISTRIBUTION AND RICHNESS PATTERNS OF BIRD COMMUNITIES IN THE HIGH ELEVATION FORESTS OF VIRGINIA

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ABSTRACT

Island biogeography theory predicts that the patterns and distributions of spatially isolated populations are governed by large scale processes. The high elevations forests in the Southern Appalachians represent a series of naturally fragmented islands that harbor many isolated populations of species at the southern limits of their range. Understanding the governing forces of population dynamics in this region will enhance the probability of species persistence in the face of threats such as global warming and human development. We surveyed bird populations across multiple elevations in Virginia and combined this with a multi-scale habitat analysis to determine influences of species presence and species richness. We detected 101 species across the elevational gradient, including 12 species with special conservation status and ten species whose presence increased with increasing elevation. These ten elevation sensitive species responded to habitat variables at both the microhabitat and landscape scale, with species-specific patterns of habitat variable correlation emerging. Habitat type was least effective in predicting species presence for any elevation sensitive species. Species richness declined over the elevational gradient until the highest elevations, where this trend reversed and richness began to increase. This pattern was driven by an increase in short-distance migrants beginning at mid-elevations, which ultimately overpowered a corresponding decrease in long-distance migrants beginning at similar elevations. Habitat analysis linked these patterns to a preference of short-distance migrants for smaller, more isolated non-forested patches, and a historical lack of persistence for long-distance migrants.

Conservation and management decisions for the region should focus on a multi-scale approach that preserves all habitat types for continued species presence and high species richness, although the persistence of particular elevation sensitive species is compounded by unique species-habitat relationships and the perception of islands as species-specific. Continued monitoring of these fragmented populations in light of both short- and long-term threats which span multiple scales of influence will maintain high species richness and ensure the persistence of crucial breeding habitat.

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INTRODUCTION

The complex distribution patterns of species organized as multiple isolated populations are addressed by island biogeography theory (MacArthur and Wilson 1963, MacArthur 1972) and the dynamics between them are addressed by metapopulation theory (Hanksi 1999). Both theories emphasize the interconnectedness of spatially segregated populations and predict that patterns of species distribution and richness will be governed by large scale spatial patterns and changes. As a result, any attempt to study species distribution patterns and dynamics of these populations should take into account not only local habitat factors but also regional patterns that may influence how local populations interact with each other (for example, through source-sink dynamics) and ultimately determine individual distributions.

Naturally isolated populations can occur as a result of evolutionary processes, such as the isolation of mountaintops over long time scales to form island habitats. Mountaintop environments were originally described as fragmented islands by Brown (1971), with high-elevation habitat surrounded by a matrix of different habitat that may or may not act as a barrier to individual movements of resident species (Ricketts 2001, Kupfer et al. 2006). One such example of this occurs in the Southern Appalachians of eastern North America. Habitat patches on these mountaintops were isolated at the end of the Pleistocene Era, when the range of many species contracted northward and upward in elevation as glaciers retreated northward (Delcourt and Delcourt 1987, Ashworth and Hoganson 1993). The result in the Southern

Appalachians is a series of remnant, isolated ecosystems in the high elevations that harbor unique or rare species at the southern edge of their range (Oosting and Billings 1951, Rabenold 1978, White and Buckner 1993).

The high elevation islands in this region are currently vulnerable to both long-term and short-term threats. Large-scale climate change has resulted in increased global temperatures (IPCC 2007), which can lead to greater range contraction or extinction of high elevation species (McCarty 2001, Wilson et al. 2005, Thomas et al. 2006, Beckage et al. 2008). In addition, these areas are threatened by small-scale human activities, including housing development and more specifically wind turbine construction, which may potentially impact the behavior of species that reside in or migrate through high elevation ridges (Larsen and Madsen 2000, Barrios and Rodriguez 2004). These threats may also influence regional plant communities that in turn impact wildlife populations, as they harbor many regionally rare wildlife species such as northern flying squirrels, several species of salamanders and many neotropical migrant birds (Haney et al. 2001, Odom et al. 2001, Ford et al. 2002). Improving management and conservation strategies within the area requires increased knowledge of what species inhabit the regions, how species presence relates to the surrounding habitat and how species-habitat relationships contribute to the population dynamics that would be altered by these threats.

While modeling species-habitat relationships has been common in ecological literature (Jones 2001, Scott et al. 2002), an increased awareness that species respond to the environment at multiple spatial scales has led to studies that seek to determine which scale is most appropriate for describing species-habitat relationships. Traditionally the relationship between species distribution and habitat has focused on the microhabitat scale, considering only habitat characteristics that are in the immediate vicinity of an individual's territory or home range (Carothers et al. 1974, Cody 1985, Urban and Smith 1989), although recent studies have attempted to include the influences of landscape and regional scales as well (Flather and Sauer 1996, Boulinier et al. 2001, Thompson et al. 2002, Wood et al. 2006). There is, however, conflicting evidence from studies specifically evaluating the importance of microhabitat characteristics versus landscape characteristics in predicting species distribution or abundance (Saab 1999, Mitchell et al. 2001, MacFaden and Capen 2002, Westphal et al. 2003, Loehle et al. 2005). Current discussions agree on the necessity of using multi-scale studies to capture the majority of variation that may be influencing species presence (Jokimaki and Huhta 1996, Mitchell et al. 2001, Lee et al. 2002, Willis and Whittaker 2002, Rahbek 2005). This issue is particularly relevant given the potential impact of both climate change and human-induced habitat change across a range of both temporal and spatial scales.

Songbirds (Passeriformes) in particular have often served as model organisms to understand species-habitat relationships within fragmented systems (e.g. Cooper and Walters 2002, Donovan and Flather 2002, Brotons et al. 2003, Betts et al. 2006). As study organisms they are ubiquitous and relatively easy to detect, and can provide valuable information on the broader state of the ecosystem. As there is little concurrence on the relative extent to which microhabitat and landscape characteristics influence forest breeding birds (Lynch and Whigham 1984, Robbins et al. 1989a, Hagan and Meehan 2002, Lichstein et al. 2002), further research in this area is required to understand forest breeding bird distribution and persistence over time. This understanding will enable land managers to predict how both climate driven and anthropogenic changes within high-elevation patches and the surrounding landscape would affect bird populations, and will enhance planning for conservation purposes.

The purpose of this study was to conduct a comprehensive inventory of bird species that breed in high elevation forests of the Southern Appalachians and to determine which habitat characteristics at multiple spatial scales best predict the distribution of elevation sensitive species. Although there have been some studies of wildlife communities in high elevation forests in the Great Smoky Mountains National Park and North Carolina (Rabenold 1978, Ford et al. 2002, Crespi et al. 2003, Sauer et al. 2008), less attention has been given to high elevation habitats in Virginia that occur as smaller, lower islands and are therefore more immediately threatened by higher temperatures (Atwood et al. 1996, MacFaden and Capen 2002). Virginia contains multiple isolated high elevation peaks with minimal amounts of remnant forests such as conifer patches (dominated by *Picea rubens* and *Abies fraseri*) and northern hardwood patches (dominated by *Acer saccharum, Fagus grandifolia* and *Betula spp.*). Any changes in available breeding habitat due to either large-scale effects such as climate charge or small-scale effects such as wind turbine construction would impact rates of colonization and extinction for bird populations in the region. A more specific knowledge of which habitat characteristics species respond and at what scale those characteristics are most important would identify the extent to which species are restricted to those habitat islands. Such knowledge could provide managers with improved methods for addressing both long-term and short-term threats that have the potential to permanently alter the ecosystem.

METHODS

Study Area

We surveyed 36 sites in Virginia that consisted of land above 1060 m (3500 ft.) in elevation and at least 30 ha in size (Figure 1.1). All sites included some public land in one of the following areas: the George Washington and Jefferson National Forest, Shenandoah National Park, Mt. Rogers National Recreation Area, Grayson-Highlands State Park, Hidden Valley Wildlife Management Area (WMA), Clinch Mountain WMA or Highland WMA. One site included a portion of private land owned by The Nature Conservancy. The majority of each site consisted of public forest (12-100%, average 70.1%) (Table 1.1). The cut-off elevation of 1060 m was chosen to encompass all high elevation habitats as well as transition forest into lower elevations.

Bird Surveys

We planned survey routes within each site to create one census point per 35 hectares of public land. When all high elevation land is considered, our sample intensity averaged one point per 62 hectares (ranging from 7-144 ha) (Table 1.1). Within each site, we determined the number of points to be surveyed and divided them into routes that were 5-15 points long. All routes were placed on hiking trails, old logging roads or gated dirt/gravel Forest Service roads, with the exception of two routes that were located on gravel public roads (Sites 31 and 28). Points were located at least 200 m apart to ensure independence (Ralph *et al.* 1995). The location of each point was recorded in the Universal Transverse Mercator (UTM) coordinate system using a hand-held GPS unit (Garmin GPS III, Garmin International, Olathe, KS).

Bird surveys were conducted during the breeding seasons from 2005-2007. Sites were divided into three sections of Virginia (northern, central, and southwest), with each section surveyed during a single year. Surveys were conducted no earlier than May 20 and no later than July 1, and were conducted within four hours of dawn and in reasonable weather, to maximize the probability that most breeding individuals would be present and singing (Ralph *et al.* 1995) . At each point one observer recorded all individuals heard or seen within 10 minutes at an unlimited radius. Effort was made to avoid double counting any individual, especially if the individual could still be heard at an adjacent point. All surveys were repeated twice within a season in approximately the same order. Surveys were conducted by ten different observers and in most cases the same observer performed both surveys of the same route. In addition, five routes (Sites 4, 5 and 7) were surveyed twice all three years by the same observer.

Habitat Surveys

Microhabitat Surveys

At each survey point we constructed a 0.04 ha (11 m radius) circular plot. Within each plot we placed two transect lines along north-south and east-west headings and recorded 15 observations of canopy cover and ground cover at randomly placed meter points along the transects. At each point, canopy cover was recorded as either open or closed, and ground cover was recorded as leaf litter, rock, woody debris, moss/lichen or herbaceous . Within the plot we also recorded the species and diameter at breast height (dbh) of each tree (> 8 cm dbh) and the number of individuals of each species of shrub (< 8 cm dbh and > 1 m height) (James and Shugart 1970)(Table 1.2).

Habitat Categories

We obtained 1:24,000-scale Digital Elevation Model (DEM) data from the USGS National Elevation Dataset (http://seamless.usgs.gov/index.php) for Virginia and West Virginia. These data were used to determine the elevation, slope and aspect of each survey point (Table 1.2). Aspect was transformed according to Beers et al. (1966). We obtained land cover data from the Southeast Gap Analysis Project (SEGAP) for Virginia (http://www.basic.ncsu.edu/segap/). Cell size was increased to 100 m and majority smoothing performed on each cell to improve processing ability of the dataset using ArcGIS, v. 9.2 (Environmental Research Systems Institute, Redlands CA). The original 253 classes of data were combined into four habitat types (coniferous, mesic deciduous, xeric deciduous/coniferous and non-forested) and each point was classified accordingly.

In addition I classified forest cover type at each point as one of 18 categories based on standard protocol used by the Virginia Department of Game and Inland Fisheries to create a more local habitat category (Table 1.3). This resulted in two habitat classifications for each point: habitat type and forest cover type.

Landscape Level Surveys

At each point I calculated diversity of habitat types and area of habitat patch in which the point was located within a one km radius using ArcGIS. Since the territory sizes of many songbirds are less than two ha in size (Freemark *et al.* 1995), the one km spatial scale should be adequate for determining landscape level effects from the perspective of a bird. I also calculated distance to the next nearest patch of the same habitat type as well as habitat proximity (defined as the sum of each patch's area divided by its distance to the point) using FRAGSTATS (McGarigal *et al.* 2002) (Table 1.2).

Statistical Analysis

Detections were converted into presence/absence records for all species. A species was recorded as present if it was detected at the point at least once, regardless of the number of times the species was detected over multiple sampling dates or the number of individuals of that species detected. All statistical analysis was done using program R (R Development Core Team 2006).

Elevation Sensitive Species

I performed a linear mixed model regression for all species predicting presence as a function of elevation. I used only points from sites where the species was present and included site as a random factor to control for clustering of points within sites. Species whose presence significantly increased ($p < 0.05$) with increasing elevation were termed elevation sensitive. Only forest-breeding birds were considered (as designated by Poole 2005), as the majority of surveys were targeted toward and carried out in forest habitat.

Since each species may have a unique response to elevation and its concurrent habitat, I created species-specific elevation patches based on the occurrence curve over the range of elevation for each elevation sensitive species (Liu et al. 2005, Jimenez-Valverde and Lobo 2007). I performed a logistic regression to calculate the probability of species occurrence as a function of elevation for each site where the species was present, and then averaged all regression lines from each site into one probability curve. I then determined the proportion of points at which the species was present out of all points surveyed. The elevation at which the average probability curve equaled the proportion of points at which the species was present overall was considered the elevation threshold and used to define the elevation patch (Figure

1.3). All area above the threshold can be considered available breeding habitat for that particular species. For each elevation sensitive species I calculated the distance to the next nearest elevation patch and the total area of all elevation patches within a one km radius, both of which are unique to each species, using FRAGSTATS (Table 1.2).

RPI vs. Elevation

A surrogate method for accounting for biological effects of elevation has been developed for Virginia using a Relative Phenology Index (RPI) (S. Klopfer, pers comm). Based on Hopkin's Bioclimatic Law (Hopkins 1920), the timing of biological events such as leafing out in spring or flower budding can be traced across geographic space using a combination of elevation and latitude, both which are commonly accepted gradients for biological differences. A 1:24,000-scale Digital Elevation Model (DEM) from the USGS National Elevation Dataset was used as a base layer to generate a cell by cell index in Virginia, with the Dismal Swamp National Wildlife Refuge used as a zero value low-elevation starting point, to a maximum value of 51 at Mt. Rogers in Wythe County. I calculated a Pearson's r correlation coefficient to look at the correlation between RPI and elevation. I also used RPI as a surrogate for elevation in modeling to compare the two measures in their effectiveness at predicting species presence.

Spatial autcorrelation

To determine if spatial autocorrelation was strong enough to influence species presence between points (Legendre and Legendre 1998, Dormann 2007), I looked for possible correlation both graphically and statistically. I plotted semivariograms for each species with the residuals of a generalized linear model that used elevation to predict species presence. Semivariograms provide a graphical representation of the spatial correlation between sampling points based on the variance in measure with distance between all pairs of sampled locations (Fortin and Dale 2005). Residuals were plotted against distance lags of 300 m (each survey point was no more than 300 m apart) up to one km to look for repetition in patterns of correlation for all species. To determine if any spatial autocorrelation that existed was statistically significant, I ran two regression models using elevation to predict species presence that were identical except that one included a spatial autocovariate term and one did not (Augustin et al. 1996). The autocovariate term was modeled assuming a spherical correlation pattern, which is the most common pattern of spatial autocorrelation observed (Armstrong 1998). Models were run as linear mixed-effects models with site as a random factor, using the penalized quasi-likelihood method (package glmmPQL in program R) (Dormann 2007).

Semivariograms for all elevation sensitive species showed little consistent pattern across distances (Figure 1.4). There were no significant differences between models that included an autocovariate term and those that did not in terms of determining which individual species were elevation sensitive. I interpreted this as evidence that spatial autocorrelation was not influencing the probability of species presence and did not include any correction for spatial autocorrelation in further analyses.

Detection probability

Recent studies have drawn attention to the potential bias introduced in census studies by failure to detect individuals that are actually present (MacKenzie et al. 2002, Tyre et al. 2003, MacKenzie 2006). Nondetection may be correlated with site or sampling covariates, which can lead to false negatives and result in biased estimates of data parameters such as local colonization and extinction probabilities and species turnover rates (MacKenzie et al. 2003, Gu and Swihart 2004, Wintle et al. 2004, Martin et al. 2005). For most species in this study, two visits per sampling point did not result in enough data to generate reliable estimates of detection with sufficiently low standard errors using program PRESENCE (Hines 2006). High standard errors may result from a combination of low detectability and high occupancy, although it would be difficult to interpret results without more visits to each sampling location. Several of the elevation sensitive species have been shown to have relatively high detectability rates in other studies (e.g. Dettmers et al. 1999, Farnsworth et al. 2002, Kissling and Garton 2006). I controlled for the potential bias in varying detectability among different habitat types by including local habitat characteristics in models (Betts *et al.* 2007).

Species-habitat Modeling of Elevation Sensitive Species

I computed a covariance matrix between all continuous microhabitat and landscape variables to test for collinearity. All variables had a Pearson's r correlation coefficient < 0.7 and were therefore retained for the models.

For each elevation sensitive species I examined the relationship between species presence and habitat at two scales: the point (microhabitat) and the landscape. In addition, I added the two measures of habitat (habitat type and forest cover type) to determine whether habitat classification alone was effective in predicting species presence. This led to three models for each species: one using microhabitat variables, one using landscape variables, and one using habitat classification variables. I performed a stepwise logistic regression to determine the most significant set of variables within each of the three candidate models and chose the best-fit model using Akaike's information criterion (AIC) (Burnham and Anderson 2002). Lower AIC values indicate a more parsimonious model, taking into account both the number of model parameters and the model fit. The stepwise logistic regression proceeded by removing each variable one at a time and then ranking all resulting models by AIC relative to the original model.

Once I obtained the set of best-fit variables for each of the three scales, I used them to create multi-scale models. This generated an additional four models, leading to seven models per species: micro, landscape, habitat, micro + landscape, micro + habitat, landscape + habitat and micro + habitat + landscape. I performed an identical stepwise logistic regression on the combination models as well, using the same data set as for the individual scale models. These seven models were ranked by AIC value and the top model for each species was then fit into a linear mixed model using site as a random factor to determine which model terms were most significant in predicting species presence. This final model was run to control for the clustering of points within a site. Elevation was not included as a variable in the models for two reasons: first, many habitat characteristics can be considered surrogate measurements of the elevation gradient, and second, two landscape level variables were calculated based on elevation (elevation patch area and distance to next elevation patch).

RESULTS

Species distribution

We surveyed 1,095 points and made 25,155 individual detections (Table 1.4). The total detections are not a count, as individual birds may have been detected twice during repeat sampling. We detected 95 species (Table 1.5), 12 of which are listed as special status species by the Virginia Department of Game and Inland Fisheries (VDGIF 2006): one is listed as a federal species of concern (Cerulean Warbler [*Dendroica cerulea*]), two are listed as state threatened (Peregrine Falcon [*Falco peregrinus*], Bald Eagle [*Haliaeetus leucocephalus*]) and nine are listed as state special concern (Alder Flycatcher [*Empidonax alnorum*], Brown Creeper [*Certhia americana*], Golden-crowned Kinglet [*Regulus satrapa*], Hermit Thrush [*Regulus satrapa*], Magnolia Warbler [*Dendroica magnolia*], Mourning Warbler [*Oporornis philadelphia*], Purple Finch [*Carpodacus purpureus*], Red-breasted Nuthatch [*Sitta canadensis*] and Winter Wren [*Troglodytes troglodytes*]).

The majority of all surveyed points (56%) fell into one forest cover type category (upland hardwoods) and a similar majority (57%) were in one habitat type category (xeric coniferous/deciduous) (Table 1.6). These two habitat classification schemes contained 57% and 62% of all observations, respectively.

Elevation Sensitive Species

Nine forest-breeding species were elevation sensitive: Black-capped Chickadees (*Poecile atricapillus*), Chestnut-sided Warblers (*Dendroica pensylvanica*), Dark-eyed Juncos (*Junco hyemalis*), Eastern Towhees (*Pipilo erythrophthalmus*), Golden-crowned Kinglets, Hermit Thrushes (*Catharus guttatus*), Red-breasted Nuthatches, Winter Wrens and Yellow-rumped Warblers (*Dendroica coronata*) (Table 1.7). All of these species were also elevation sensitive when RPI was used in place of elevation, and in addition Canada Warblers (*Wilsonia canadensis*) were elevation sensitive when using RPI. Canada Warblers are included in all further analyses. Elevation and RPI had a high correlation coefficient value of 0.66. As a result I chose to use elevation in all further analyses, as it is a simpler measurement of gradient, although RPI values are also reported where appropriate. An example plot used to determine elevation sensitivity is shown in Figure 1.2. Elevation threshold values for each species were calculated and range from 890 m to 1300 m (Table 1.8, Figure 1.3).

Species-habitat modeling

For nine of the ten elevation sensitive species, the model containing all three scales had the lowest AIC value (Table 1.9). The exception was Eastern Towhees, where the model excluding landscape had the lowest ranking AIC. Differences of Δ AIC < 2 are considered not significant according to Burnham and Anderson (2002).

For five species (Dark-eyed Juncos, Hermit Thrushes, Red-breasted Nuthatches, Winter Wrens, Yellow-rumped Warblers) the top ranking model with all three scales was equivalent to the second highest ranking model, which included only the microhabitat and landscape scales, indicating that habitat class was insignificant. In these cases the Δ AIC between the top two models was zero except for Red-breasted Nuthatches, where Δ AIC between the top two models was 1.753. Of these five species, for three (Dark-eyed Juncos, Hermit Thrushes, Red-breasted Nuthatches) all models that included the landscape scale ranked highest, for one (Yellow-rumped Warblers) all models that included the microhabitat scale ranked highest and for one (Winter Wrens) all models that included both the microhabitat and the landscape scale ranked highest.

For the remaining four species (Black-capped Chickadees, Canada Warblers, Chestnut-sided Warblers, Golden-crowned Kinglets) the top model containing all three scales was significantly different from the second-ranking model. For two of these (Canada Warblers, Chestnut-sided Warblers) all models that included the microhabitat scale ranked highest, for one (Golden-crowned Kinglets) all models that included the landscape scale ranked highest and for one (Black-capped Chickadees) all models that included both the microhabitat and the landscape scale ranked highest. Thus, in these cases as well, habitat was secondary to landscape and microhabitat variables. The final species (Eastern Towhees) had only microhabitat and habitat in the top model; the second ranking model included all three scales and the top four models all included the microhabitat scale. In this case the landscape scale was secondary.

Results of the linear mixed models run for each species using the most significant model are shown in Table 1.10, with several variables highly significant to multiple species (Figures 1.5 and 1.6). In many cases, variables were retained despite not being considered statistically significant in the final linear mixed model. All variables were included in at least one final regression model for at least one species. For three of the four species (Golden-crowned Kinglets, Hermit Thrushes, Red-breasted Nuthatches) where all models including landscape were the top-ranking models, the most important variable was the area of the elevation patch, the exception being Dark-eyed Juncos. Occurrence of these four species was never significantly linked to proximity to the nearest similar habitat patch or elevation patch. Significance of individual variables was much more variable for the four species (Canada Warblers, Chestnut-sided Warblers, Eastern Towhee, Yellow-rumped Warblers) where models including microhabitat were the top-ranking models. Landscape and microhabitat scales were equally important to Black-capped Chickadees and Winter Wrens, and significance of individual variables varied widely between these two species. In only three species (Black-capped Chickadees, Golden-crowned Kinglets, Red-breasted Nuthatches) were any individual habitat class variables significant, and in all cases p-values were relatively high, although still less than 0.05. Four variables were not significant in any model, although each was retained in a regression model for at least one species: aspect, distance to water, tree density and habitat patch area.

DISCUSSION

Our surveys revealed a high level of avian species richness within this region of the Southern Appalachians. Of the 95 species we encountered, ten elevation sensitive species comprise the subset of avifauna most likely to be influenced by changes in high elevation forests. Their response to the elevational gradient implies that their species-habitat relationship is unique in high elevation forests, even though not all ten species are species of conservation concern or have limited extent of range. Five of the ten elevation sensitive species (Dark-eyed Juncos, Eastern Towhees, Chestnut-sided Warblers, Black-capped Chickadees and Canada Warblers) were among the 20 most detected species. Dark-eyed Juncos and Eastern Towhees were the third and fourth most frequently detected species, respectively, and were encountered at both the lowest and highest elevations surveyed (Table 1.5). Although the rarest species were encountered so infrequently that limited inference can be made about whether they are elevation sensitive, these results show that response to the elevational gradient is not restricted only to uncommon species or species with limited extent of range.

Most sampling was concentrated in a relatively small number of habitats: generally in xeric forests and more specifically in upland hardwood (Table 1.6). The distribution of sampling points reflects the relative abundance of different forest types in high elevation regions; thus, results from this study are more appropriate for interpretation in the region as a whole rather than for specific habitat types that are regionally rare. This may be in part why our two categories classifying habitat were relatively less important than other scales, and models that included habitat often did no better than the same model excluding habitat (Table 1.9). This also may explain why three elevation sensitive species (Golden-crowned Kinglets, Red-breasted Nuthatches, Winter Wrens) that are considered habitat specialists (Poole 2005) did not show a strong association with either habitat classification category, and the two species that showed a significant relationships to habitat (Golden-crowned Kinglets, Red-breasted Nuthatches) were not linked to the coniferous forests to which they are considered habitat specialists (Table 1.10). Regardless of sampling scheme, however, using only forest community type at any scale seems to be an ineffective way to predict species presence (Cushman *et al.* 2008), and neither the size of the habitat patch nor the distance to the next similar habitat patch were crucial for any species. This may have crucial implications for management plans, because it implies that establishing a preferred habitat type (for example, creating more open balds) to increase the richness of overall species or elevation sensitive species would not be effective without also considering both microhabitat and landscape factors.

The multi-scale approach is particularly useful in this region where the combined threats of climate change and human development occur on both small and large scales. Previous studies have supported using a multi-scale approach to habitat assessment (Saab 1999, Thompson et al. 2002, Seoane et al. 2004), and this study contributes to the view that it is not an either-or question but a matter of the extent to which many scales of habitat are biologically relevant to the species-habitat relationship. The variation in significance of habitat variables across multiple scales and multiple species implies that species response to current threats will be seen in changing distribution of individuals and ultimately disruption of regional population dynamics. Species richness throughout the region as a whole may be negatively impacted by both local and regional habitat disturbance.

For the three species usually described as habitat specialists in coniferous forests (Golden-crowned Kinglets, Red-breasted Nuthatches, Winter Wrens), landscape level variables played a more prominent role in their distribution, in particular the proportion of land within one km that was above the individual species' elevation threshold . A fourth species, Hermit Thrushes, which are usually described as less strongly specialized in breeding habitat (Poole 2005), also showed a similar relationship with this variable. These four species had the four highest elevation thresholds (Table 1.9). For these species, then, the degree to which they perceive their surrounding environment as an island or group of islands is most influential in determining their distribution. Area of this island is a more important factor than the characteristics of the forests that compose it. The dynamics of these populations will be more influenced by the quantity of island habitats within the high elevations rather than the quality of the forests within and would be most affected by large scale habitat disturbances such as range retraction that would reduce the number of islands.

Three of the four species (Eastern Towhees, Chestnut-sided Warblers, Yellow-rumped Warblers) whose top models all included the microhabitat scale are usually described as edge species or species that prefer open stands (Poole 2005). The fact that they are elevation sensitive at all may be due to the lack of forest openings or edge habitat until the very highest elevations, where forest gives way to rocky ground, open balds and dense understory thickets. Understory composition (as measured by whether the dominant shrub species was evergreen) and density proved to be prominent factors among these species, as well as among Canada Warblers, which may be because in the high elevations the understory is increasingly defined by thickets of rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) (Wiser *et al.* 1996). The presence of these two shrub species tends to inhibit tree density (Monk *et al.* 1985), thereby limiting canopy closure. The dominance of microhabitat variables over landscape variables suggests that local disruptions of habitat such as wind turbine construction would affect individual presence, and that the persistence of mixed habitat with open balds is crucial to the persistence of these species' populations.

The two remaining species (Black-capped Chickadees, Dark-eyed Juncos) are both considered habitat generalists (Poole 2005) and show varied patterns of correlation. Black-capped Chickadees show a relationship with all three scales and most notably show a strong negative association with habitat diversity and a strong positive association with evergreen understory. This suggests they prefer continuous forest with a dense understory and are less dependent on island habitats than on overall landscape pattern. The high prevalence of Dark-eyed Juncos (at 828 of 1095 points, 76%) combined with the lack of strong correlation with any individual variables or set of variables at one scale suggests that Dark-eyed Juncos are high elevation generalists adapted to multiple habitats and habitat characteristics. The reason they are elevation sensitive may have less to do with habitat and more with variables not considered in this study (e.g. interspecific competition). The generality of these two species points towards better adaptation to habitat disturbance on any scale, although they still maintain a positive response to high elevation regions. The population dynamics of these two species out of all elevation sensitive species might be the lest interrupted by habitat disturbance of any kind.

Based on the variation in species-habitat relationships of the elevation sensitive species, we can make management recommendations toward which specific sites are of lowest and highest conservation value. The number of species and specifically elevation sensitive species is greatest at Sites 4-10 (Reddish Knob and surrounding sites) and Sites 30-34 (Mt. Rogers and surrounding sites) (Table 1.11). These sites are comprised of large patches of high elevation habitat with numerous surrounding island patches, which would be particularly important for species who strongly respond to increasing island area such as Golden-Crowned Kinglets, Hermit Thrushes, Red-breasted Nuthatches and Winter Wrens (Table 1.10). Mt. Rogers in particular contains the only significant portion of conifer forest surveyed. In addition, Sites 26, 27 and 29 (Hidden Valley and surrounding sites) show high levels of species richness, and the availability of edge habitat along gravel roads throughout these sites may be beneficial to species which prefer dense understory such as Canada Warblers and Chestnut-sided Warblers. We consider these three regions to be of high conservation priority for high elevation bird communities within the state.

In contrast, Site 1 (Cow Knob), Site 23 (Sugar Run Mt.) and Sites 13 and 15-19 (Mt. Pleasant and surrounding sites) have fewer species and are small, isolated patches. Populations within these particular sites are already limited and are the most likely to be negatively impacted as climate change decreases island size. Along with these, Sites 2 and 3 (Shenandoah National Park) and Site 36 (Peaks of Otter) also have low conservation value, although attraction of tourists to these sites makes them less likely to be directly influenced by human development. The absence of high elevation habitat at these groups of sites would cause minimal impact on elevation sensitive species.

Finally, Relative Phenology Index (RPI) may be a useful substitute for elevation as a measurement of the gradient to which species respond, especially in study regions which span a wide latitudinal range. Threshold values used to determine the difference between available and non-available habitat using elevation were closely tied to results using RPI (Table 1.9). While elevation provides a more direct approach to defining the gradient along which species distribution vary, RPI may be a more accurate assessment, as it takes into account not only elevational difference but also latitudinal differences. That is, a habitat that is found at a certain elevation in the southern part of the state may be found at lower elevations in the northern part of the state due to the latitudinal difference, and RPI would be an appropriate measure to capture this variation.

In conclusion, the distribution of elevation sensitive species is determined by much more than broad forest classification. In high elevation forests, the definition of an "island" is dynamic and can be very species specific even within the same taxa that inhabit the same region. Differences in the importance of regional island pattern versus local habitat composition means that species distribution and richness patterns are being governed not only by processes involving island biogeography and metapopulation dynamics but also processes that apply to even non-fragmented populations. Further intensive surveys and analyses in other similar regions of the Southern Appalachians (e.g. high elevation forests in North Carolina and Tennessee) would provide a more wide-ranging database with which to examine the patterns reported here and see if they hold true throughout the larger region. Continued monitoring of surveyed populations as well as baseline studies on unexamined high elevation lands would be necessary to ensure population persistence in this ecologically valuable region.

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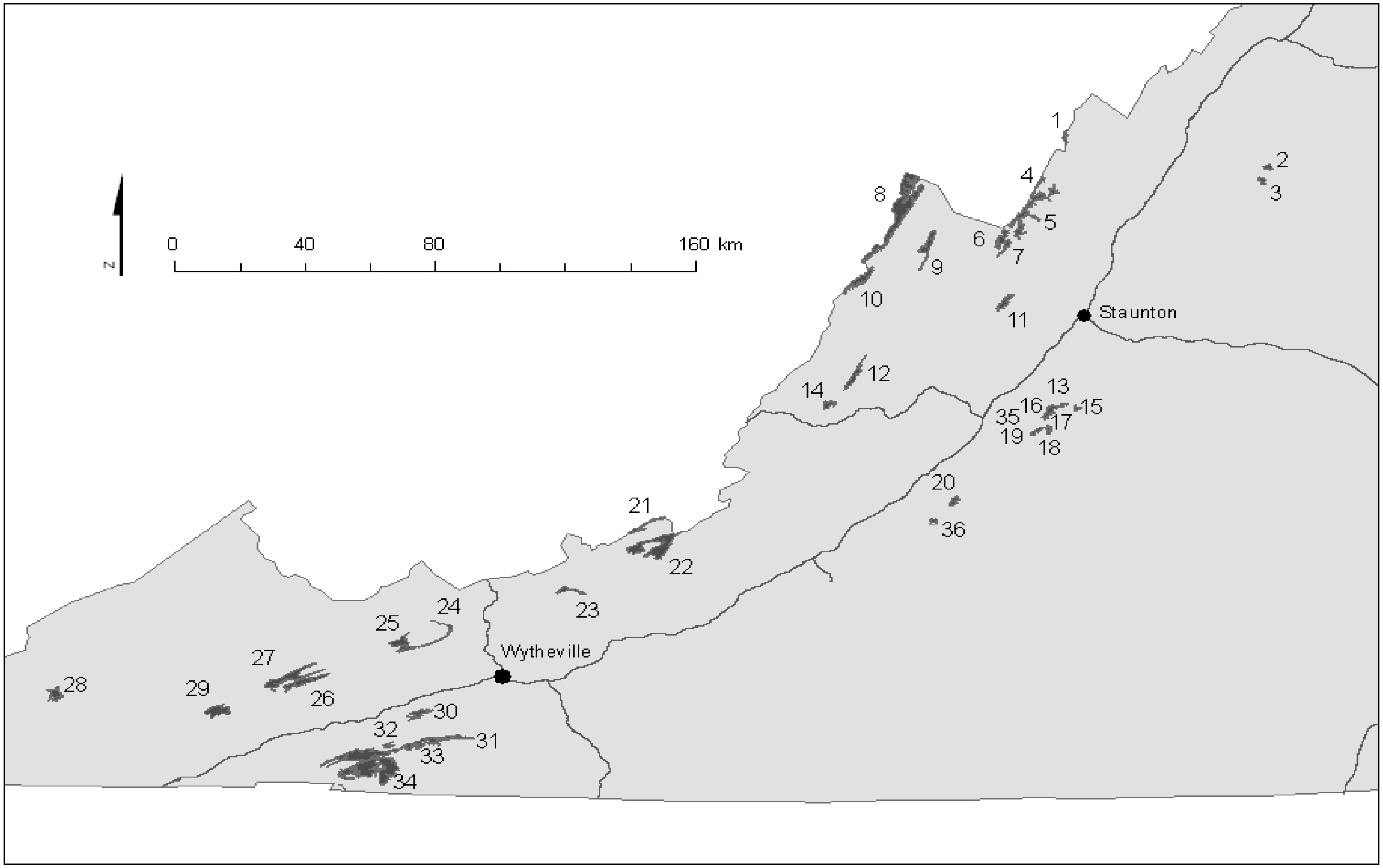

Figure 1.1 Location of high elevation sites surveyed from 2005-2007. See Table 1.1 for site identities and descriptions.

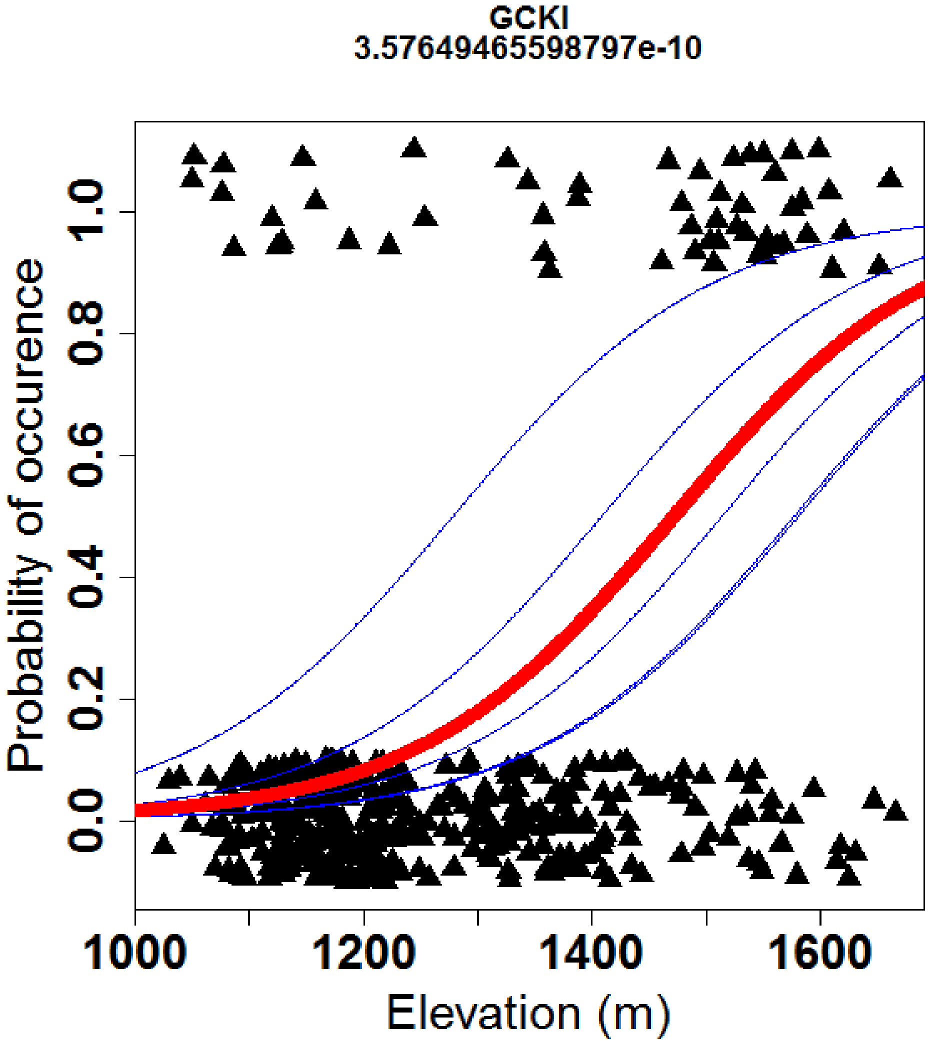

Figure 1.2. Logistic regression curve for Golden-crowned Kinglets, a species that is elevation sensitive. Thin lines represent the regression curve for each individual site where the species was present, and the thick line represents the average of all these sites. Each triangle represents a survey point. Points are jittered along the y-axis at 0 and 1 to allow for easier interpretation. Number below the species code represents the p-value for the average regression line.

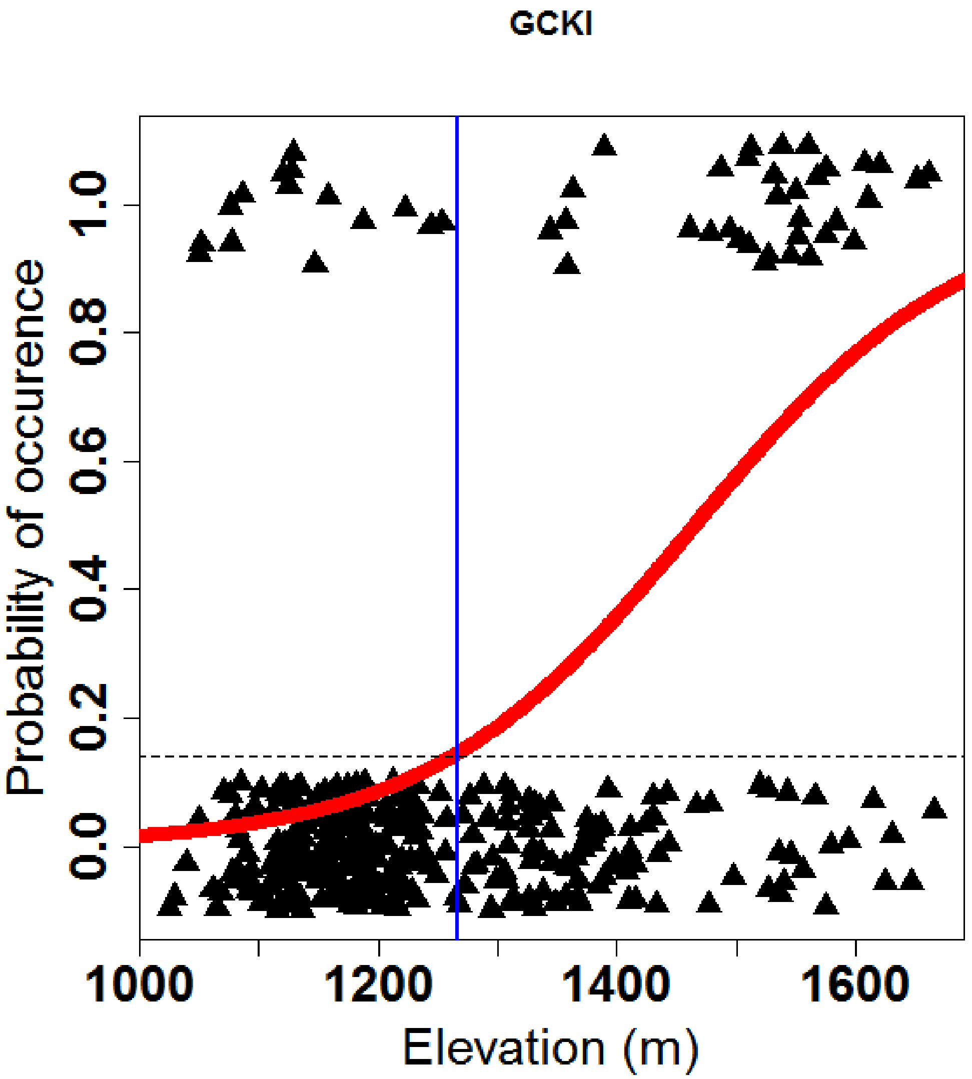

Figure 1.3. Estimation of threshold elevation for Golden-crowned Kinglets. Thick line represents the average logistic regression curve for predicting species presence at all sites where the species was present. Dashed line represents the proportion of all points at which the species was detected. Thin line represents the elevation value where the regression line and percent occurrence are equivalent, or, the elevation threshold.

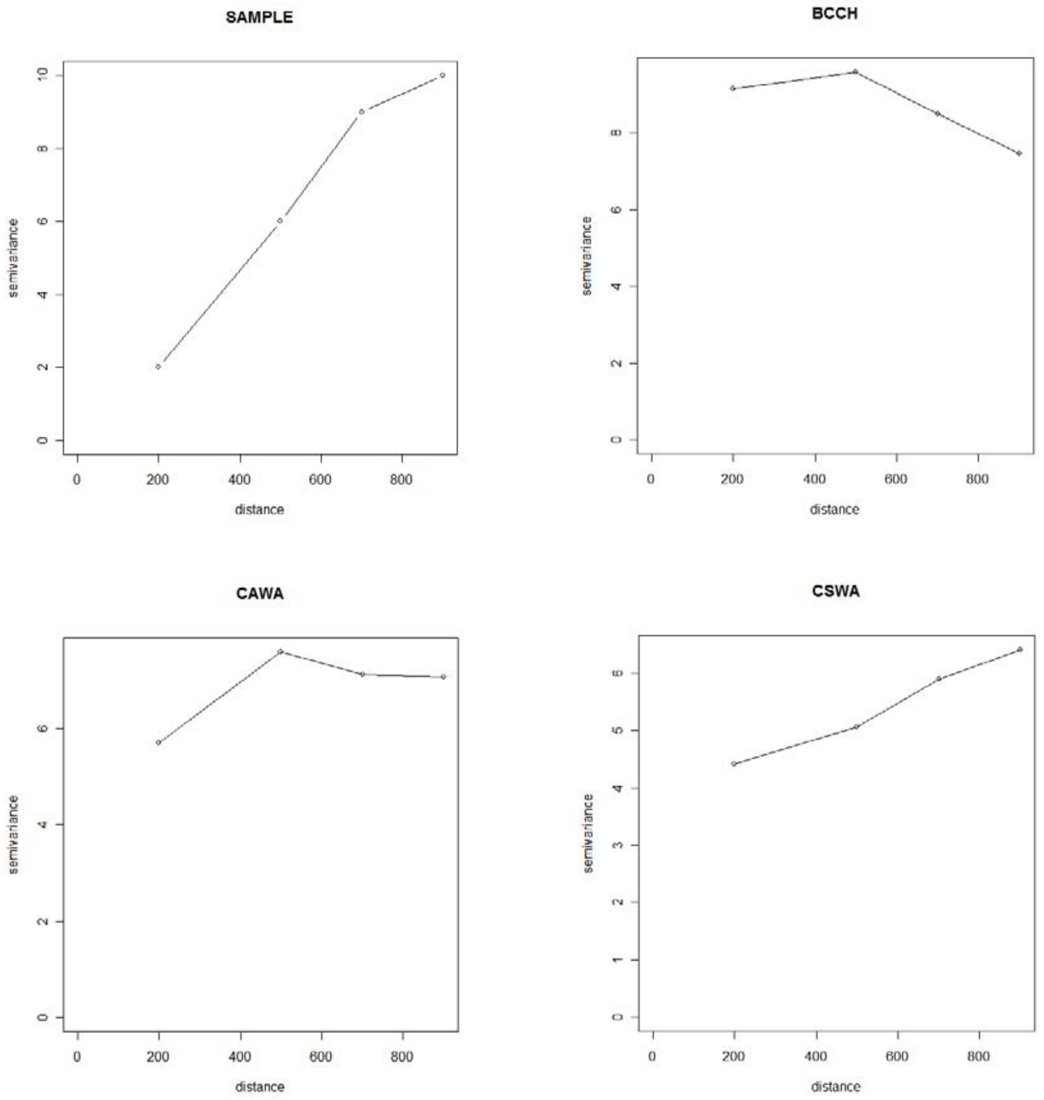

Figure 1.4. Semivariogram plots for elevation sensitive species. Semivariance between points is plotted at distance lags of 300 m, which represent the distance categories used to check for spatial correlations in species presence between points. Total distance assessed is 1000 m. First plot shows example of positive spatial autocorrelation: a consistent pattern similar to this among all species would indicate that spatial autocorrelation was a significant factor in determining species presence.

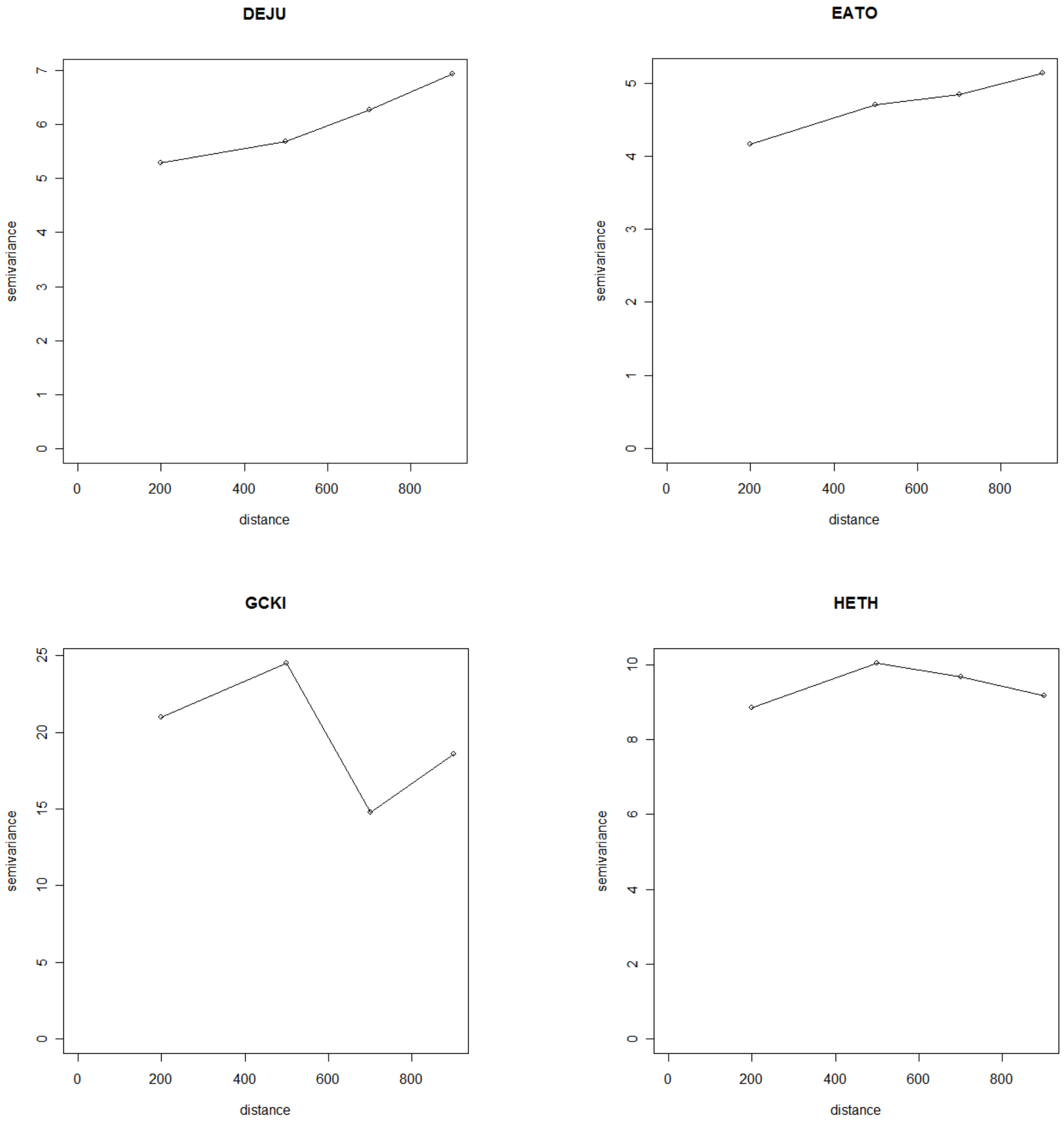

Figure 1.4. con't.

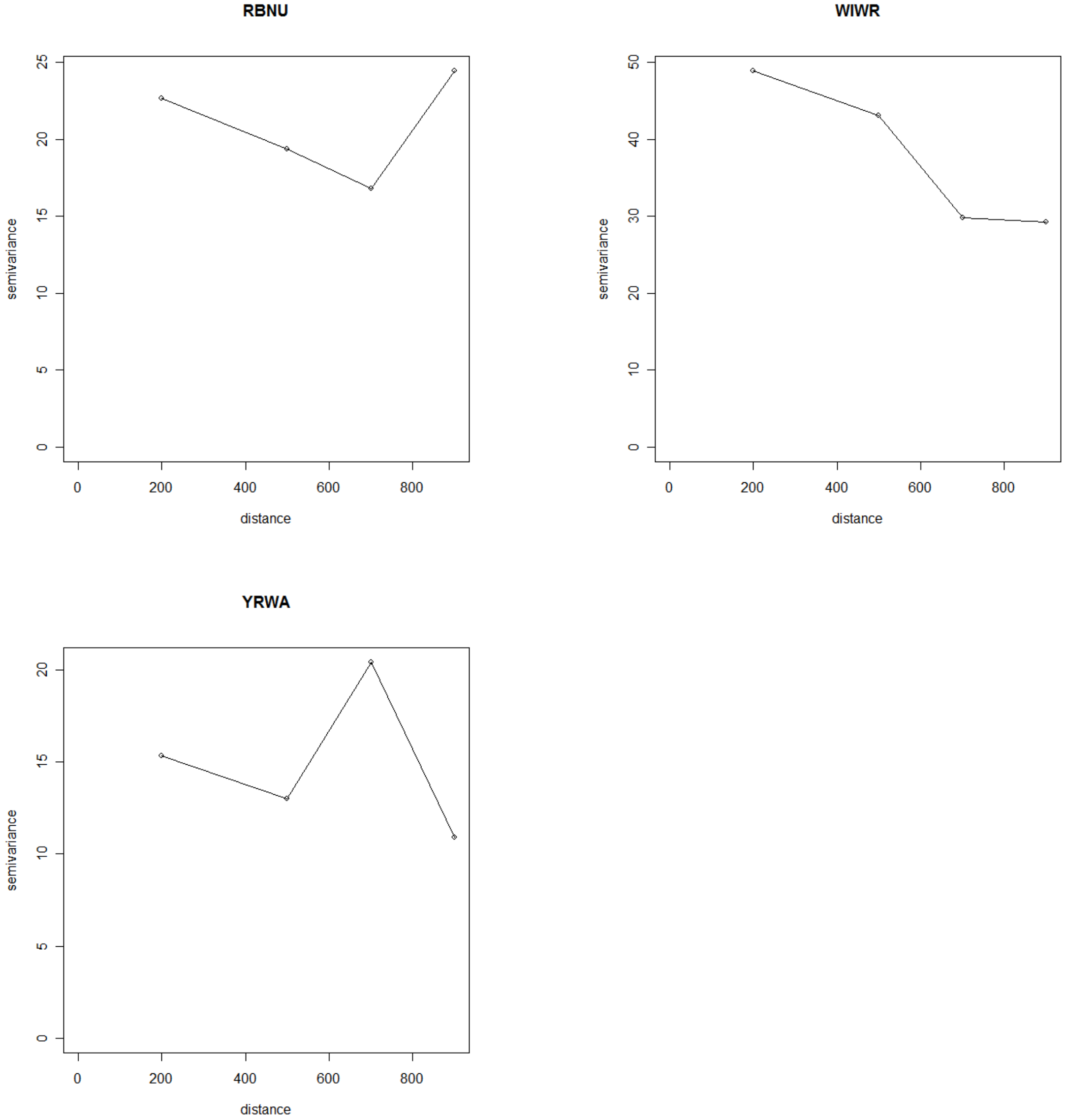

Figure 1.4. con't.

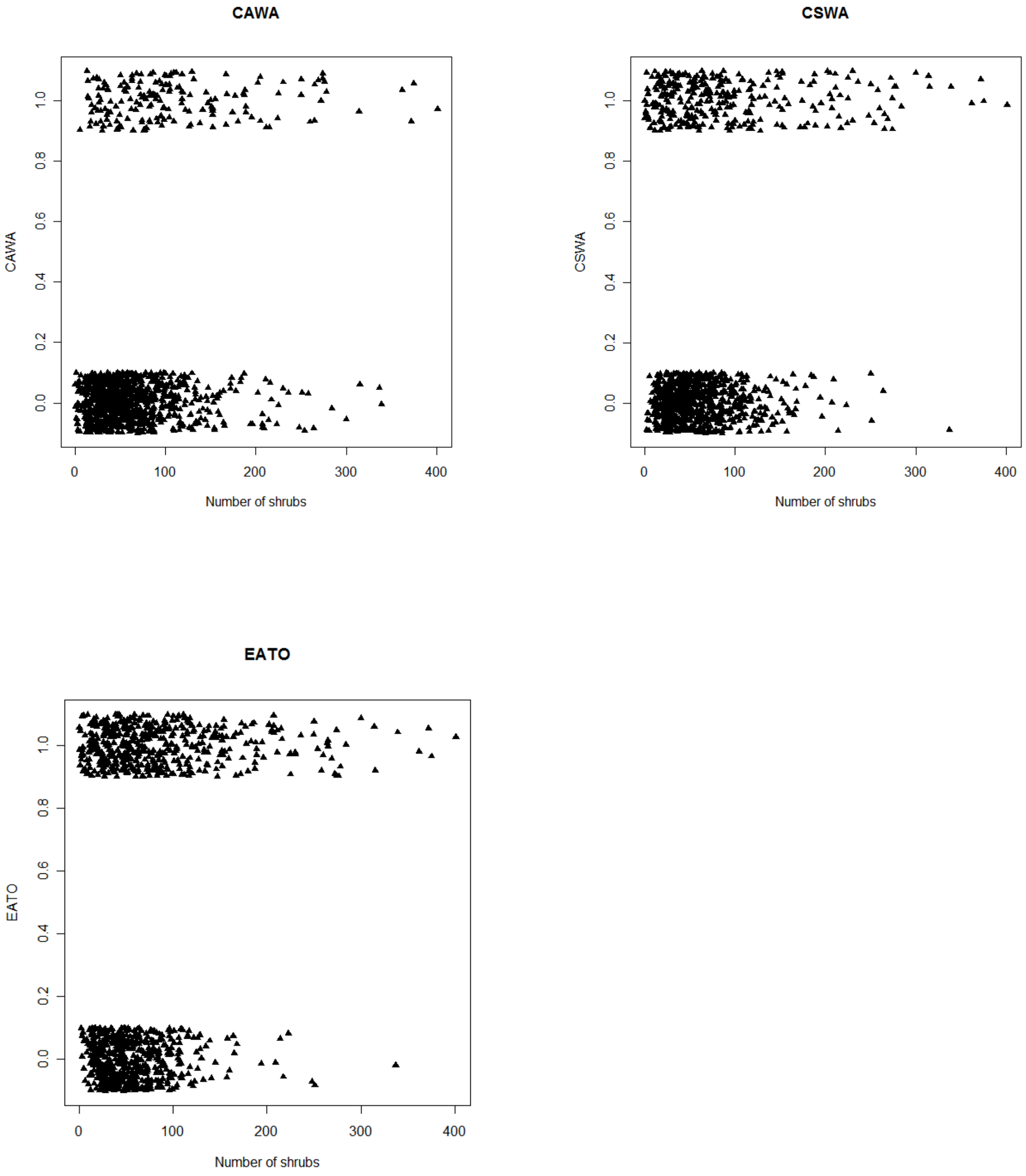

Figure 1.5. Relationship between number of shrubs and presence of three species most highly correlated with variable.

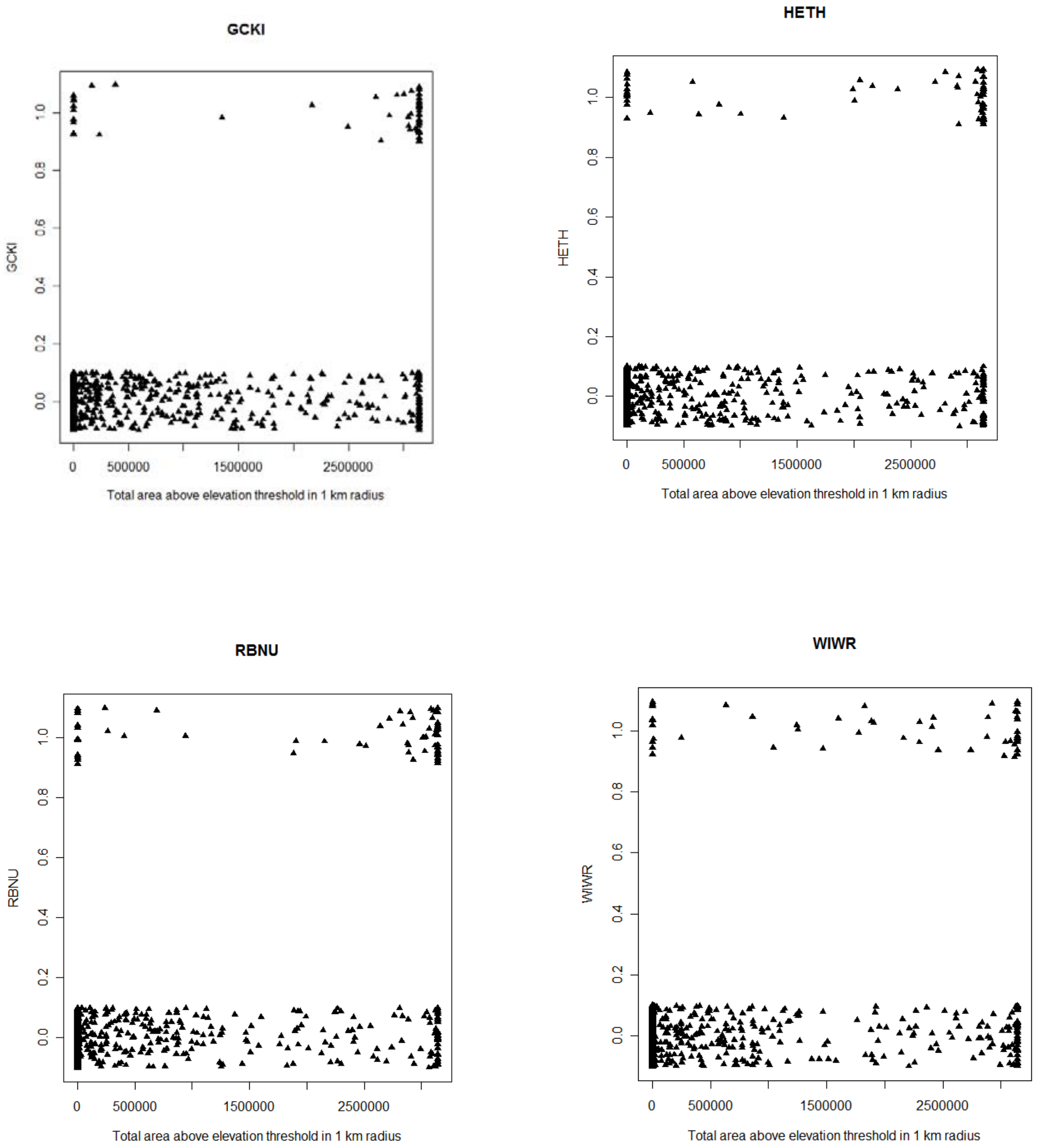

Figure 1.6. Relationship between total area of elevation threshold for each species and presence of four species most highly correlated with variable.

Table 1.1. Location, size and number of points sampled for all sites.

Site ID	Site Name	County	Total area (ha) >3500 ft.	% Public	Points Sampled	Average area (ha) surveyed per point
1	Cow Knob	Rockingham	54.04	14.63	5	11
2	Stoney Man	Page	327.57	99.24	15	22
3	Hawksbill Mt.	Page	315.95	99.3	15	21
4	Middle Mt.	Rockingham	93.18	38.53	15	6
5	Reddish Knob	Augusta	2991.22	80.85	45	66
6	Freezland Flat	Augusta	194.17	98.39	10	19
7	Hardscrabble Knob	Augusta	1313.64	98.8	30	44
8	Laurel Forks	Highland	3378.47	36.03	45	75
9	Sounding Knob	Highland	897.08	54.53	25	36
10	Paddy Knob	Highland	1157.49	63.83	30	39
11	Elliot Knob	Augusta	872.63	98.07	25	35
12	Warm Springs Mt.	Bath	142.93	11.49	20	7
13	Maintop Mt.	Nelson	31.52	19.99	5	6
14	Warm Springs Mt. South	Allegheny	577.78	96.49	15	39
15	The Priest	Nelson	165.98	80.67	10	17
16	Elk Pond Mt.	Nelson	446.82	49.37	20	22
17	Cold Mt.	Amherst	163.6	50.26	10	16
18	Mt. Pleasant	Amherst	325.51	98.71	15	22
19	Bald Knob	Amherst	138.22	98.77	10	14
20	Apple Orchard Mt.	Botetourt	375.51	71.24	15	25
21	Peters Mt.	Giles	1252.33	58.31	25	50
22	Salt Pond Mt.	Giles	5498.01	93.9	125	44
23	Sugar Run Mt.	Giles	847.19	86.85	25	34
24	Garden Mt. East	Bland	1628.16	42.4	20	81
25	Garden Mt. West	Bland	4315.43	41.18	30	144
26	Flat Top Mt.	Smyth	2290.46	80.09	40	57
27	Clinch Mt.	Russell	4809.18	65.57	45	107
28	High Knob	Wise	1588.17	69.95	15	106
29	Hidden Valley	Washington	3134.99	60.02	40	78
30	Glade Mt.	Smyth	1031.53	92.56	25	41
31	Comer's Rock	Wythe	393.98	97.95	20	20
32	Bobby's Ridge	Smyth	276.18	97.72	15	18
33	Straight Mt.	Smyth	5049.1	45.91	40	126
34	Mt. Rogers	Grayson	20914.53	60.47	235	89
35	Tarjacket Ridge	Amherst	550.41	72.51	10	55
36	Peaks of Otter	Bedford	57.22	100	8	7

Table 1.2. Habitat variables measured at three scales for each point surveyed.

Scale of analysis	Variable	Description
Micro	aspect	transformed between 0 and 2 (2 = northeast, 0 = southwest)
	slope	degrees
	waterDist	distance to water, 1 = 0-25m, 2 = 25-50m, 3 = >50m
	roadDist	distance to forest edge 1 = 0-25m, 2 = 25-50m, 3 = >50m
	edgeDist	distance to public road, 1 = 0-25m, 2 = 25-50m, 3 = >50m
	canopyClass	% canopy coverage, 1 = 0-25, 2 = 25-50, 3 = 50-75, 4 = 75-100
	domGround	dominant ground cover, H = herb, L = leaves, R = rock, M = moss/lichen, W = wood
	totalTreeS	total number of tree species
	totalTreeN	total number of trees
	totalShrubS	total number of shrub species
	totalShrubN	total number of shrubs
	shrub1SConifer	presence/absence of understory dominated by evergreens
	HW	% hardwood based on ratio of conifer to deciduous diameter of top 3 tree species
Habitat	habType	1 of 4 classifications based on SEGAP data (see text)
	coverType	1 of 18 classifications based on VDGIF protocol (see text)
Landscape	habArea	area (ha) of habitat patch in which point is located
	habDiv	number of different habitat types within 1 km of point (0-4)
	habProx	fragmentation index using Proximity function in FRAGSTATS, 1 km radius
	habENN	distance to next nearest habitat patch of same type
	patchArea	area (ha) of land above threshold elevation within 1 km of point
	patchENN	distance to next nearest patch above threshold elevation

Table 1.3. Classification scheme used by the Virginia Department of Game and Inland Fisheries to classify forest cover type.

Code	Cover Type Description
MO	three or more mixed oak species
UH	mixed upland hardwoods (oaks, red and sugar maple, beech, hickories, black cherry, black locust)
CH	mixed lowland hardwoods or cove hardwoods (poplar, birches, red maple, magnolias, black cherry, basswood, ash)
NH	birch, beech, maples
RO	northern red oak
WO	white oak
CO	chestnut oak
H	hickory (all species)
HEM	hemlock (all species)
B	black or yellow birch
M	maple (red or sugar)
SLP	shortleaf/pitch pine
VP	Virginia pine
WP	white pine
LT	laurel/rhododendron thicket
O	sod clearing/opening
DT	deciduous thicket
SPR	spruce/fir

Table 1.4. Summary of sampling by year.

	2005	2006	2007	Total
Public Area(ha) surveyed > 3500 ft.	14290	23444	10339	48073
Sites	21	8	7	36
Census points	390	365	340	1095
Observations	8949	8550	7656	25155
Species detected	85	80	75	95

Table 1.5. Summary of all bird species detected.

Species	Scientific Name	Observations	Sites	Points
Acadian Flycatcher	*Empidonax virescens*	69	14	48
Alder Flycatcher	*Empidonax alnorum*	1	1	1
American Crow	*Corvus brachyrhynchos*	570	34	319
American Goldfinch	*Carduelis tristis*	245	26	167
American Redstart	*Setophaga ruticilla*	323	32	183
American Robin	*Turdus migratorius*	277	24	160
Bald Eagle	*Haliaeetus leucocephalus*	2	1	1
Baltimore Oriole	*Icterus galbula*	1	1	1
Barn Swallow	*Hirundo rustica*	3	1	1
Barred Owl	*Strix varia*	12	9	12
Black Vulture	*Coragyps atratus*	3	1	2
Black-and-white Warbler	*Mniotilta varia*	826	35	479
Black-billed Cuckoo	*Coccyzus erythropthalmus*	53	10	43
Blackburnian Warbler	*Dendroica fusca*	52	7	31
Black-capped Chickadee	*Poecile atricapillus*	409	20	187
Black-throated Blue Warbler	*Dendroica caerulescens*	560	31	288
Black-throated Green Warbler	*Dendroica virens*	1028	22	445
Blue Jay	*Cyanocitta cristata*	511	34	316
Blue-gray Gnatcatcher	*Polioptila caerulea*	42	14	30
Blue-headed Vireo	*Vireo solitarius*	1146	35	593
Broad-winged Hawk	*Buteo platypterus*	26	12	23
Brown Creeper	*Certhia americana*	21	2	18
Brown Thrasher	*Toxostoma rufum*	7	5	7
Brown-headed Cowbird	*Molothrus ater*	57	19	37
Canada Warbler	*Wilsonia canadensis*	355	27	176
Carolina Chickadee	*Poecile carolinensis*	26	7	23
Carolina Wren	*Thryothorus ludovicianus*	2	2	2
Cedar Waxwing	*Bombycilla cedrorum*	221	21	103
Cerulean Warbler	*Dendroica cerulea*	2	2	2
Chestnut-sided Warbler	*Dendroica pensylvanica*	917	33	318
Chimney Swift	*Chaetura pelagica*	46	12	32
Chipping Sparrow	*Spizella passerina*	77	12	33
Common Raven	*Corvus corax*	220	22	132
Common Yellowthroat	*Geothlypis trichas*	16	4	12
Dark-eyed Junco	*Junco hyemalis*	2108	36	828
Downy Woodpecker	*Picoides pubescens*	134	30	120
Eastern Bluebird	*Sialia sialis*	5	4	5
Eastern Phoebe	*Sayornis phoebe*	36	16	29

Table 1.5. con't.

Species	Scientific Name	Observations	Sites	Points
Eastern Screech Owl	*Megascops asio*	3	3	3
Eastern Towhee	*Pipilo erythrophthalmus*	1601	36	506
Eastern Tufted Titmouse	*Baeolophus bicolor*	217	26	151
Eastern Wood Pewee	*Contopus virens*	598	33	384
Field Sparrow	*Spizella pusilla*	121	8	56
Golden-crowned Kinglet	*Regulus satrapa*	134	6	55
Gray Catbird	*Dumetella carolinensis*	165	23	96
Great Blue Heron	*Ardea herodias*	1	1	1
Great Crested Flycatcher	*Myiarchus crinitus*	213	22	113
Great Horned Owl	*Bubo virginianus*	1	1	1
Hairy Woodpecker	*Picoides villosus*	217	28	165
Hermit Thrush	*Catharus guttatus*	88	7	63
Hooded Warbler	*Wilsonia citrina*	179	17	110
Horned Lark	*Eremophila alpestris*	1	1	1
House Wren	*Troglodytes aedon*	17	3	9
Indigo Bunting	*Passerina cyanea*	561	30	279
Kentucky Warbler	*Oporornis formosus*	1	1	1
Killdeer	*Charadrius vociferus*	1	1	1
Least Flycatcher	*Empidonax minimus*	146	10	57
Magnolia Warbler	*Dendroica magnolia*	117	9	70
Mallard	*Anas platyrhynchos*	13	2	7
Mockingbird	*Mimus polyglottos*	1	1	1
Mourning Dove	*Zenaida macroura*	132	19	89
Mourning Warbler	*Oporornis philadelphia*	7	1	4
Northern Bobwhite	*Colinus virginianus*	16	4	11
Northern Cardinal	*Cardinalis cardinalis*	22	10	19
Northern Flicker	*Colaptes auratus*	141	23	126
Northern Parula	*Parula americana*	13	6	12
Northern Rough-winged Swallow	*Stelgidopteryx serripennis*	1	1	1
Ovenbird	*Seiurus aurocapilla*	2361	36	778
Peregrine Falcon	*Falco peregrinus*	6	3	5
Pileated Woodpecker	*Dryocopus pileatus*	249	32	177
Pine Warbler	*Dendroica pinus*	10	5	6
Purple Finch	*Carpodacus purpureus*	2	1	2
Red-bellied Woodpecker	*Melanerpes carolinus*	27	12	25
Red-breasted Nuthatch	*Sitta canadensis*	111	8	73
Red-eyed Vireo	*Vireo olivaceus*	2763	36	865
Red-shouldered Hawk	*Buteo lineatus*	4	4	4
Red-tailed Hawk	*Buteo jamaicensis*	17	7	11
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	633	33	314
Ruby-throated Hummingbird	*Archilochus colubris*	24	14	24
Ruffed Grouse	*Bonasa umbellus*	60	14	44
Scarlet Tanager	*Piranga olivacea*	1079	35	593
Song Sparrow	*Melospiza melodia*	21	5	14
Swainson's Thrush	*Catharus ustulatus*	1	1	1

Table 1.5 con't.

Species	Scientific Name	Observations	Sites	Points
Tree Swallow	*Tachycineta bicolor*	22	3	4
Turkey Vulture	*Cathartes aura*	75	12	33
Veery	*Catharus fuscescens*	1495	33	584
White-breasted Nuthatch	*Sitta carolinensis*	254	29	178
Wild Turkey	*Meleagris gallopavo*	25	7	21
Winter Wren	*Troglodytes troglodytes*	73	10	52
Wood Thrush	*Hylocichla mustelina*	278	29	204
Worm-eating Warbler	*Helmitheros vermivorum*	97	15	63
Yellow-bellied Cuckoo	*Coccyzus americanus*	147	17	113
Yellow-bellied Sapsucker	*Sphyrapicus varius*	92	9	64
Yellow-rumped Warbler	*Dendroica coronata*	89	14	55
Yellow-throated Vireo	*Vireo flavifrons*	6	6	6

Table 1.6. Prevalence of each forest cover type and habitat type surveyed.

Habitat Category	Code	Description	Points	Sites	Observations	Species
Cover Type	B	black or yellow birch	10	4	231	44
	CH	cove hardwoods	107	19	2263	71
	CO	chestnut oak	10	5	359	48
	DT	deciduous thicket	4	1	85	21
	H	hickory	4	2	103	20
	HEM	hemlock	13	6	340	52
	LT	laurel or rhododendron thicket	7	3	171	32
	M	maple	28	10	598	60
	MO	three or more mixed oak species	34	12	861	52
	NH	birch, beech, maples	80	7	1419	58
	O	sod clearing/opening	22	6	594	49
	RO	northern red oak	92	23	2320	68
	SLP	shortleaf/pitch pine	9	5	417	43
	SPR	spruce/fir	11	2	258	38
	UH	mixed upland hardwoods	617	35	14326	85
	VP	virginia pine	2	1	99	24
	WO	white oak	2	2	31	17
	WP	white pine	6	4	146	34
Habitat Type	1	Non-forested	47	7	1015	71
	2	Xeric deciduous/coniferous	628	36	15702	88
	3	Mesic deciduous	395	24	7880	73
	4	Mesic coniferous	4	1	97	19

Table 1.7. Species that are elevation sensitive i.e. species presence significantly increased with elevation. (*) Indicates species was not elevation sensitive when using elevation but was elevation sensitive when using RPI. See text for details.

Species	Slope	Intercept	p-value
Black-capped Chickadee	0.0023	-3.8226	0.036
Canada Warbler *	-0.0004	-0.8950	0.670
Chestnut-sided Warbler	0.0028	-3.8305	0.003
Dark-eyed Junco	0.0050	-4.7147	< 0.001
Eastern Towhee	0.0029	-2.7583	< 0.001
Golden-crowned Kinglet	0.0089	-13.0432	< 0.001
Hermit Thrush	0.0076	-11.6209	< 0.001
Red-breasted Nuthatch	0.0075	-11.5800	< 0.001
Winter Wren	0.0060	-10.1300	< 0.001
Yellow-rumped Warbler	0.0073	-10.6509	< 0.001

Table 1.8. Threshold elevation values for each elevation sensitive species used to define landscape level elevation patches.

Common Name	Prevalence	Threshold (Elev - m)	Threshold(RPI)
Black-capped Chickadee	0.22	1190	38
Canada Warbler	0.19	1210	37
Chestnut-sided Warbler	0.30	1070	34
Dark-eyed Junco	0.75	1170	37
Eastern Towhee	0.44	890	27
Golden-crowned Kinglet	0.14	1270	41
Hermit Thrush	0.14	1290	41
Red-breasted Nuthatch	0.14	1300	41
Winter Wren	0.09	1300	42
Yellow-rumped Warbler	0.09	1180	39

Table 1.9. Summary results of stepwise logistic regression using three habitat scales to predict species presence for elevation sensitive species. See Table 1.2 for definitions of scale and model variables.

Scale	Models	K	AIC	Δ AIC	w_i	deviance
Black-capped Chickadee						
micro + habitat + land	*aspect + waterDist + roadDist + canopyClass + totalTreeS + totalTreeN + shrub1SConifer + totalShrubS + totalShrubN +coverType + habType + habArea + habDiv1km + habProx1km + habENN + patchArea1km*	16	757.48	0.00	0.89	725.5
micro + land	*aspect + waterDist + roadDist + canopyClass + totalTreeS + totalTreeN + shrub1SConifer + totalShrubS + totalShrubN + habArea + habDiv1km + habProx1km + habENN + patchArea1km*	14	761.67	4.19	0.11	735.7
micro + habitat	*aspect + waterDist + roadDist + canopyClass + totalTreeS + totalTreeN + shrub1SConifer + totalShrubS + totalShrubN + coverType + habType*	11	789.19	31.71	0.00	754.6
habitat + land	*coverType + habType + habArea + habDiv1km + habProx1km + habENN + patchArea1km*	7	804.57	47.09	0.00	765.2
land	*habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	6	817.30	59.82	0.00	805.3
micro	*aspect + slope + waterDist + roadDist + edgeDist + canopyClass + domGround + totalTreeS + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN*	13	834.83	77.35	0.00	806.8
habitat	*coverType + habType*	2	862.15	104.67	0.00	820.2

Scale	Models	K	AIC	Δ AIC	w_i	deviance
Canada Warbler						
micro + habitat + land	*slope + waterDist + roadDist + canopyClass + domGround + totalTreeN + shrub1SConifer + totalShrubN + coverType + habType + habArea + habProx1km + patchArea1km + patchENN*	14	768.00	0.00	0.87	726.0
micro + land	*slope + waterDist + roadDist + canopyClass + domGround + totalTreeN + shrub1SConifer + totalShrubN + habArea + habProx1km + patchArea1km + patchENN*	12	771.79	3.79	0.13	731.8
micro + habitat	*slope + waterDist + roadDist + canopyClass + domGround + totalTreeN + shrub1SConifer + totalShrubN + coverType + habType*	10	785.83	17.83	0.00	747.8
micro	*aspect + slope + waterDist + roadDist + edgeDist + canopyClass + domGround + totalTreeS + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN*	13	788.84	20.83	0.00	756.8
habitat + land	*coverType + habType + habArea + habProx1km + patchArea1km + patchENN*	6	856.32	88.31	0.00	808.3
habitat	*coverType + habType*	2	885.08	117.07	0.00	843.1
land	*habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	6	885.79	117.79	0.00	875.8

Table 1.9 con't.

Scale	Models	K	AIC	Δ AIC	w_i	deviance
Chestnut-sided Warbler						
micro + habitat + land	*slope + waterDist + roadDist + edgeDist + domGround + totalTreeS + shrub1SConifer + totalShrubN + coverType + habType + habDiv1km + habProx1km + patchArea1km*	13	975.51	0.00	0.98	903.5
micro + land	*slope + waterDist + roadDist + edgeDist + domGround + totalTreeS + shrub1SConifer + totalShrubN + habArea + habDiv1km + habProx1km + patchArea1km*	12	983.36	7.86	0.02	947.4
micro + habitat	*slope + waterDist + roadDist + edgeDist + domGround + totalTreeS + shrub1SConifer + totalShrubN + coverType + habType*	10	986.51	11.00	0.00	916.5
micro	*aspect + slope + waterDist + roadDist + edgeDist + canopyClass + domGround + totalTreeS + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN*	13	1040.87	65.36	0.00	1010.9
habitat + land	*coverType + habType + habDiv1km + habProx1km + patchArea1km*	5	1072.38	96.87	0.00	1026.4
habitat	*coverType + habType*	2	1084.61	109.10	0.00	1042.6
land	*habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	6	1119.48	143.97	0.00	1111.5

Scale	Models	K	AIC	Δ AIC	w_i	deviance
Dark-eyed Junco						
micro + habitat + land	*slope + canopyClass + totalTreeN + HW + totalShrubN + habType + habDiv1km + habProx1km + habENN*	9	510.27	0.00	0.35	496.3
micro + land	*slope + canopyClass + totalTreeN + HW + totalShrubN + habDiv1km + habProx1km + habENN*	8	510.27	0.00	0.35	496.3
land	*habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	6	512.01	1.75	0.15	504.0
habitat + land	*habType + habDiv1km + habProx1km + habENN*	4	512.01	1.75	0.15	504.0
micro	*aspect + slope + waterDist + roadDist + edgeDist + canopyClass + domGround + totalTreeS + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN*	13	519.93	9.66	0.00	503.9
micro + habitat	*slope + canopyClass + totalTreeN + HW + totalShrubN + habType*	6	519.93	9.66	0.00	503.9
habitat	*coverType + habType*	2	523.21	12.94	0.00	521.2

Table 1.9. con't.

Scale	Models	K	AIC	Δ AIC	w_i	deviance
Eastern Towhee						
micro + habitat	*slope + waterDist + edgeDist + domGround + totalTreeS + totalTreeN + shrub1SConifer + totalShrubN + coverType + habType*	10	1169.48	0.00	0.78	1107.5
micro + habitat + land	*slope + waterDist + edgeDist + domGround + totalTreeS + totalTreeN + shrub1SConifer + totalShrubN + coverType + habDiv1km + habENN + patchArea1km*	12	1172.16	2.68	0.21	1112.2
micro + land	*slope + waterDist + edgeDist + domGround + totalTreeS + totalTreeN + shrub1SConifer + totalShrubN + habDiv1km + habENN + patchArea1km*	11	1178.16	8.68	0.01	1146.2
micro	*aspect + slope + waterDist + roadDist + edgeDist + canopyClass + domGround + totalTreeS + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN*	13	1188.07	18.59	0.00	1160.1
habitat	*coverType + habType*	2	1337.11	167.62	0.00	1295.1
habitat + land	*coverType + habType + habDiv1km + habENN + patchArea1km*	5	1337.11	167.62	0.00	1295.1
land	*habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	6	1397.64	228.16	0.00	1389.6

Scale	Models	K	AIC	Δ AIC	w_i	deviance
Golden-crowned Kinglet						
micro + habitat + land	*slope + canopyClass + domGround + totalTreeS + totalTreeN + HW + totalShrubS + coverType + habType + patchArea1km + patchENN*	10	281.20	0.00	0.68	261.2
habitat + land	*coverType + habType + patchArea1km + patchENN*	4	283.70	2.50	0.20	271.7
micro + land	*slope + canopyClass + domGround + totalTreeS + totalTreeN + HW + totalShrubS + patchArea1km + patchENN*	9	285.42	4.22	0.08	267.4
land	*habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	6	286.99	5.78	0.04	281.0
micro + habitat	*slope + canopyClass + domGround + totalTreeS + totalTreeN + HW + totalShrubS + coverType + habType*	9	314.42	33.22	0.00	266.4
habitat	*coverType + habType*	2	317.21	36.01	0.00	275.2
micro	*aspect + slope + waterDist + roadDist + edgeDist + canopyClass + domGround + totalTreeS + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN*	13	360.18	78.97	0.00	334.2

Table 1.9. con't.

Scale	Models	K	AIC	Δ AIC	w_i	deviance
Hermit Thrush						
micro + habitat + land	*slope + domGround + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN + coverType + habType + habProx1km + patchArea1km*	11	309.53	0.00	0.29	299.5
micro + land	*slope + domGround + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN + habProx1km + patchArea1km*	9	309.53	0.00	0.29	299.5
habitat + land	*coverType + habType + habProx1km + patchArea1km*	4	309.89	0.36	0.25	299.9
land	*habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	6	310.69	1.16	0.16	304.7
micro + habitat	*slope + domGround + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN + coverType + habType*	9	369.72	60.19	0.00	317.7
habitat	*coverType + habType*	2	374.89	65.36	0.00	332.9
micro	*aspect + slope + waterDist + roadDist + edgeDist + canopyClass + domGround + totalTreeS + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN*	13	397.47	87.94	0.00	375.5

Scale	Models	K	AIC	Δ AIC	w_i	deviance
Red-breasted Nuthatch						
micro + habitat + land	*slope + roadDist + domGround + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN + coverType + habType + habDiv1km + habProx1km + patchArea1km*	13	316.21	0.00	0.70	294.2
micro + land	*slope + roadDist + domGround + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN + habDiv1km + habProx1km + patchArea1km*	11	317.96	1.75	0.29	302.0
habitat + land	*coverType + habType + habDiv1km + habProx1km + patchArea1km*	5	324.19	7.98	0.01	312.2
land	*habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	6	330.04	13.83	0.00	322.0
micro + habitat	*slope + roadDist + domGround + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN + coverType + habType*	10	382.81	66.60	0.00	332.8
habitat	*coverType + habType*	2	393.18	76.97	0.00	351.2
micro	*aspect + slope + waterDist + roadDist + edgeDist + canopyClass + domGround + totalTreeS + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN*	13	431.94	115.72	0.00	405.9

Table 1.9. con't.

Scale	Models	K	AIC	Δ AIC	w_i	deviance
Winter Wren						
micro + habitat + land	*slope + waterDist + edgeDist + HW + shrub1SConifer + totalShrubS + coverType + habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	13	268.17	0.00	0.50	252.2
micro + land	*slope + waterDist + edgeDist + HW + shrub1SConifer + totalShrubS + habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	12	268.17	0.00	0.50	252.2
habitat + land	*coverType + habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	7	291.26	23.10	0.00	285.3
micro + habitat	*slope + waterDist + edgeDist + HW + shrub1SConifer + totalShrubS + coverType*	7	320.13	51.96	0.00	276.1
land	*habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	6	330.04	61.87	0.00	285.3
habitat	*coverType + habType*	2	331.78	63.61	0.00	295.8
micro	*aspect + slope + waterDist + roadDist + edgeDist + canopyClass + domGround + totalTreeS + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN*	13	365.13	96.96	0.00	347.1

Scale	Models	K	AIC	Δ AIC	w_i	deviance
Yellow-rumped Warbler						
micro + habitat + land	*aspect + roadDist + canopyClass + totalTreeS + HW + shrub1SConifer + totalShrubS + coverType + habType + habDiv1km + habProx1km + patchArea1km*	12	337.89	0.00	0.50	317.9
micro + land	*aspect + roadDist + canopyClass + totalTreeS + HW + shrub1SConifer + totalShrubS + habDiv1km + habProx1km + patchArea1km*	10	337.89	0.00	0.50	317.9
micro + habitat	*aspect + roadDist + canopyClass + totalTreeS + HW + shrub1SConifer + totalShrubS + coverType + habType*	9	353.67	15.78	0.00	327.7
micro	*aspect + slope + waterDist + roadDist + edgeDist + canopyClass + domGround + totalTreeS + totalTreeN + HW + shrub1SConifer + totalShrubS + totalShrubN*	13	363.43	25.54	0.00	341.4
habitat + land	*coverType + habType + habDiv1km + habProx1km + patchArea1km*	5	372.69	34.80	0.00	330.7
land	*habArea + habDiv1km + habProx1km + habENN + patchArea1km + patchENN*	6	377.25	39.36	0.00	369.3
habitat	*coverType + habType*	2	394.55	56.66	0.00	352.6

Table 1.10. Results of mixed model logistic regression using site as a random factor for elevation sensitive species. A (+) or (-) indicates the direction of the relationship and number of (+) or (-) represents the p-value (+ < 0.05, ++ < 0.01, +++ < 0.001). Letters and numbers in parentheses for Columns G, N and O represent the category that was significant to the relationship (see Table 1.3 for cover type codes). See Table 1.2 for identities and descriptions of all variables.

	Microhabitat variables													**Habitat vars**		**Landscape variables**					
Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**	**Q**	**R**	**S**	**T**	**U**
BCCH								-			+++	-			+ (4)		---	++			
CAWA		+++	-				+ (R)		--		+++		+++								--
CSWA				-	---		--- (L)				++		+++				-				
DEJU						+											++				
EATO		+			---						+++		++								
GCKI														- (CH)						+++	
HETH																		+		+++	
RBNU							+ (R)							- (CH)	- (3)					+++	
WIWR		+++			++														+	+++	
YRWA								++		-	++						-	++			

Micro

A aspect
B slope
C waterDist
D roadDist
E edgeDist
F canopyClass
G domGround
H totalTreeS
I totalTreeN
J HW
K shrub1SConifer
L totalShrubS
M totalShrubN

Habitat

N coverType
O habType

Landscape

P habArea
Q habDiv1km
R habProx1km
S habENN
T patchArea1km
U patchENN

Table 1.11. Number of overall species and elevation sensitive species detected at each site.

Site	Name	Species	Elevation Sensitive Species
1	Cow Knob	20	5
2	Stoney Man	38	4
3	Hawksbill Mt.	33	5
4	Middle Mt.	49	6
5	Reddish Knob	57	9
6	Freezland Flat	32	6
7	Hardscrabble Knob	54	8
8	Laurel Forks	54	8
9	Sounding Knob	49	8
10	Paddy Knob	50	9
11	Elliot Knob	28	6
12	Warm Springs Mt.	39	6
13	Maintop Mt.	21	4
14	Warm Springs Mt. South	33	3
15	The Priest	27	4
16	Elk Pond Mt.	33	6
17	Cold Mt.	34	4
18	Mt. Pleasant	26	4
19	Bald Knob	28	6
20	Apple Orchard Mt.	29	4
21	Peters Mt.	38	6
22	Salt Pond Mt.	49	8
23	Sugar Run Mt.	32	4
24	Garden Mt. East	30	2
25	Garden Mt. West	42	4
26	Flat Top Mt.	44	7
27	Clinch Mt.	55	5
28	High Knob	30	3
29	Hidden Valley	45	6
30	Glade Mt.	37	6
31	Comer's Rock	40	3
32	Bobby's Ridge	41	5
33	Straight Mt.	48	5
34	Mt. Rogers	70	10
35	Tarjacket Ridge	32	4
36	Peaks of Otter	14	4

CHAPTER 2: SPECIES RICHNESS OF BIRD COMMUNITIES ACROSS AN ELEVATIONAL GRADIENT IN THE SOUTHERN APPALACHIAN FORESTS OF VIRGINIA

INTRODUCTION

The existence of an elevational gradient of species richness has long been recognized in ecology (MacArthur 1972, Stevens 1992, Lomolino 2001). Although patterns of species richness vary between taxa and regions, the number of species present tends to decrease with increasing altitude (Rahbek 1995, 2005). Multiple explanations have been proposed for altitudinal trends in species richness, which fall into the three broad categories of spatial, historical and climatic hypotheses. Spatial hypotheses focus on the effects of area in limiting species richness (Terborgh 1973, Rosenzweig 1995, Rahbek 1997), on spatial constraints such as the mid-domain effect that presents a null model for species distributions based on overlapping ranges (Colwell and Lees 2000, Colwell et al. 2004), or on the influence of spatial heterogeneity in habitat (Terborgh 1977, Rosenzweig 1992, Bohning-Gaese 1997, MacFaden and Capen 2002). Historical hypotheses focus on the role of past geological events in creating fragmented and isolated habitats which influence population dynamics and persistence over evolutionary time scales (Ricklefs and Schluter 1993, Willis and Whittaker 2000, Hawkins and Porter 2003). Climatic hypotheses highlight the role of energy and other abiotic factors (Currie 1991, Inouye et al. 2000, Bailey et al. 2004). Despite the recent abundance of studies aiming to test these hypotheses (Lomolino 2001), elevational gradient patterns are still inconsistent (Rahbek 2005) and as yet there is no consensus on which general theories best apply when explaining species richness patterns over an elevational gradient.

The Southern Appalachians of eastern North America provide a unique region in which to examine species richness over an elevation gradient. Glacial retreat at the end of the Pleistocene Era created relic habitats that can only persist at high elevations in such southern latitudes (Delcourt and Delcourt 1987, White and Buckner 1993). These naturally fragmented forests comprise a chain of mountaintop islands throughout the Southern Appalachians with community distributions to which island biogeography theory (MacArthur and Wilson 1963) and metapopulation theory (Hanksi 1999) are highly applicable. Examples of forest communities at high elevations include spruce-fir forest (dominated by *Picea rubens* and *Abies fraseri*) and northern hardwood forest (dominated by *Acer saccharum, Fagus grandifolia* and *Betula spp.*). The conservation status of these habitats is critical, as they are under immediate threat from rising temperatures because of global climate change (Sillett et al. 2000, McCarty 2001, Wilson et al. 2005, Thomas et al. 2006), human activities such as wind energy development (Barrios and Rodriguez 2004), and atmospheric pollutants (McNulty et al. 1996, Hames et al. 2002).

The bird populations in these high elevation forests are a relatively accessible and critical group in which to examine patterns of species richness. These fragments are valuable habitat for songbirds in eastern North America, many species of which are neotropical migrants whose breeding range would otherwise be restricted to more northern latitudes. The species of songbirds that breed in the Southern Appalachians are numerous (Sauer *et al.* 2008), and seemingly comprise relatively stable and persistent populations (Haney *et al.* 2001). However, there is considerable concern about current threats to the forests that may impact populations of these species. Specifically, there is concern about the wide-spread population declines (Robbins et al. 1989b, Pardieck and Sauer 2007) and sensitivity to fragmentation (Askins et al. 1990, Flather and Sauer 1996, Schmiegelow et al. 1997) observed in migratory birds. Migration status is an especially important life history trait for birds, and differences in mobility and dispersal ability among guilds impact their response to habitat fragmentation and change. Furthermore, patterns among birds may differ considerably from those of more sedentary terrestrial taxa.

The purpose of this study was to determine patterns of avian species richness across the elevational gradient in the Southern Appalachians of Virginia and quantify how these patterns relate to the surrounding habitat at multiple scales. I focused on this region because, although there has been some attention paid to bird communities to the south (Rabenold 1978, Lichstein et al. 2002, Simons et al. 2006), forests within Virginia have received little attention despite being more fragmented and isolated. I chose a multi-scale approach in looking at correlations between habitat and species richness because previous studies have demonstrated the importance of accounting for habitat variables at both local and landscape levels to capture the full explanatory power of habitat models (Saab 1999, Norton et al. 2000, Rahbek and Graves 2001, Lichstein et al. 2002, Deppe and Rotenberry 2008).

METHODS

Data Collection

We conducted point count surveys during the breeding season at 1,093 randomly selected points on public land over 1060 m (3500 ft) in Virginia from 2005-2007. An additional 248 points from the Breeding Bird Survey (BBS) conducted by the US Forest Service in Virginia from 2005-2007 (Sauer *et al.* 2008) ranging from 257 m – 1500 m were included in the study for a total of 1,341 points. Points ranged in elevation from 257 m (Sprouts Run, Botetourt Co.) to 1666 m (Wilburn Ridge, Grayson Co.). The highest elevation in the state is 1746 m (Mt. Rogers, Grayson/Smyth Cos.). Most points (996) were located within the George Washington and Jefferson National Forests, and most of the remaining points (225) were located in Shenandoah National Park, Grayson Highlands State Park or one of three state wildlife management areas (Highland WMA, Clinch Valley WMA, Hidden Valley WMA). Twenty points were located on private land owned by The Nature Conservancy.

Routes of 5-15 aggregated points were randomly placed along foot trails, old logging roads and gated gravel roads and were stratified along the elevational gradient. Surveys were conducted during the first four hours after sunrise in good weather and lasted 10 minutes per point. All individual birds heard or seen within an unlimited radius of the point were recorded. Surveys were conducted by nine different observers to minimize observer bias. All points were visited twice, either in the same season or during two of the three survey years, with the exception of 5 routes (75 points) that were visited 6 times (twice each year for three years). Surveys were conducted no earlier than

May 14 and no later than July 1 each year. Surveys were focused on forested habitat, although some sampling of edge habitat and grass balds did occur.

Habitat data were collected from 11 m radius vegetation plots at each point, and land cover data were taken from the Southeast Gap Analysis Project (SEGAP) land cover data set (Table 2.1). All data collection methods and variables recorded were the same as those used in Chapter 1. Microhabitat variables were not available for points from the BBS.

Data Analysis

All data analysis was performed using program R (R Core Development Team 2006).

Species were divided into migratory guild (long-distance migrant, short-distance migrant, resident) according to the USGS classification scheme (Gough *et al.* 1998). I excluded flyovers and aquatic species from the data set. Due to unequal sampling along the elevation gradient, cumulative totals were not calculated for any site or route smaller than the state-wide level; instead, average number of species observed at a point was used as a measure of species richness. Of the 75 points that were visited more than twice, two of the six visits were randomly selected to maintain constant sampling intensity among all points.

To determine if the sampling intensity was adequate to detect most species in the region, I plotted a species accumulation curve using random subsampling of all points. The species accumulation curve (Figure 2.1) reaches a clear asymptote with sharply decreasing confidence intervals. From this I concluded that sampling was adequate to obtain reliable measures of species richness.

I ran a multi-scale habitat analysis for overall species richness and for each migratory guild. I used a step-wise linear model combining three scales of habitat variables for each response category assuming a Poisson distribution of richness. Methods for the multi-scale habitat analysis are the same as those conducted in Chapter 1. Habitat analysis was only performed on points where complete microhabitat data were available (985 points), and was therefore restricted to elevations of approximately 1060 m and above. After a preliminary review, I repeated the same habitat analysis using only points above 1300 m (116 points), which represents the elevation above which richness patterns appear to shift among migratory guilds, to determine whether habitat correlations changed along with the shift in richness patterns.

RESULTS

We detected 101 species in 30,495 individual observations (Table 2.2). This included 49 long-distance migrants, 35 short-distance migrants and 17 residents. Twelve of the species observed are listed as special status species by the Virginia Department of Game and Inland Fisheries (VDGIF 2006). Nine are listed as state special concern (Alder Flycatcher [*Empidonax alnorum*], Brown Creeper [*Certhia americana*], Golden-crowned Kinglet [*Regulus satrapa*], Hermit Thrush [*Catharus guttatus*], Magnolia Warbler [*Dendroica magnolia*], Mourning Warbler [*Oporornis philadelphia*], Purple Finch [*Carpodacus purpureus*], Red-breasted Nuthatch [*Sitta canadensis*], Winter Wren [*Troglodytes troglodytes*]), two are listed as state threatened (Peregrine Falcon [*Falco* *peregrinus*], Bald Eagle [*Haliaeetus leucocephalus*]) and one is listed as a federal species of concern (Cerulean Warbler [*Dendroica cerulea*]). These special status species showed little correlation, as they were detected across almost all elevations and varied greatly in elevational range and mean elevation (Table 2.3).

Overall species richness significantly declined with increasing elevation until 1400 m ($\beta = -0.0052$, s.e. = 0.0005, $p \leq 0.001$), after which richness significantly increased ($\beta = 0.0148$, s.e. = 0.0051, $p = 0.005$) (Figure 2.2). Species richness response to elevation differed significantly according to migratory guild. Richness of long-distance migrants did not change until 1100 m, at which point it significantly decreased ($\beta = -0.0022$, s.e. = 0.0001, $p \leq 0.001$) (Figure 2.3). Short-distance migrants showed a divergent pattern, with richness constant until 1100 m, after which it significantly increased ($\beta = 0.0024$, s.e. = 0.0002, $p \leq 0.001$) (Figure 2.4). Resident species showed a consistent decrease in richness with no change in slope direction at 1100 m or any other elevation (Figure 2.5).

Overall species richness, richness of long-distance migrants and richness of residents showed a significant negative relationship with elevation, while richness of short-distance migrants showed a significant positive relationship (Table 2.4). Among all guilds and overall richness, seven out of 19 habitat variables from all three scales stood out as consistently significant. Significant variables from the microhabitat scale were distance to water, distance to road, tree density and the presence of a coniferous understory. The only significant variable in the habitat category was cover type. Significant variables from the landscape scale were habitat diversity and distance to next similar habitat patch. With the exception of habitat diversity, the correlation between richness and the variable was in the same direction among all guilds and overall richness: positive for distance to water, presence of an evergreen understory and distance to next similar habitat patch, and negative for distance to road, tree density and certain cover types. Adjusted R^2 values ranged from 0.26 for short-distance migrants to 0.08 for residents.

The correlations between richness and habitat variables shifted when the habitat analysis was run using only points above 1300 m (Table 2.5). Only long-distance migrant richness and short-distance migrant richness showed a significant relationship with elevation. The most significant habitat variable for all response groups was cover type, with only two other variables (distance to road, habitat diversity) remaining significant among the groups. Adjusted R^2 values showed greater variation, ranging from 0.53 for short-distance migrants to 0.01 for residents.

DISCUSSION

The monotonic decline in species richness that we observed over the elevational gradient is commonly reported (Rahbek 1995, Rosenzweig 1995, Rahbek 2005), although the change in pattern at higher elevations indicates an uncommon shift in factors influencing richness at higher elevations. The limited range of elevation throughout the study region limits the probability that richness is being driven by spatial considerations. With an elevational span of less than 1500 m, it is unlikely that species ranges are expansive enough along the gradient to generate a random peak of species richness at mid-elevations as predicted by the mid-domain effect (Colwell and Lees 2000, Colwell et al. 2004), and in fact I saw no peak of species richness in mid-elevations. Regional habitat heterogeneity is also limited, with the state-wide mountainous area dominated by general mixed hardwood forest interspersed with relatively fewer patches of conifer forest and a small number of open balds (Fleming et al. 2001). This lack of strong habitat diversity over the entire region surveyed leads me to suggest that this is not a major driver in the observed pattern of species richness.

Area effects are also a commonly considered influence on species richness patterns, in that richness tends to decline with elevation due to a decrease in available area (Rahbek 1997, Sanders 2002, McCain 2007, Romdal and Grytnes 2007). As species richness did, in general, decrease with elevation, this hypothesis remains relevant to this study, but we did not test it directly. The structure of the landscape differs from that of systems in which area effects have been reported (Sanders 2002, Vetaas and Grytnes 2002, McCain 2007), and the fact that there were more species in more isolated habitat patches is inconsistent with this hypothesis. A precise estimation of area would necessitate clear delineation between mountaintops, which is strongly lacking in this region. The physiographic nature of the region, being continuous ridge and valley formations (Smith 1994), means that while the highest elevations are isolated peaks and high elevation habitat is clearly defined, much of the elevational range we surveyed is continuous over multiple mountains. It would be arbitrary to define either an elevation band or study region boundary. Regardless of sampling difficulties, however, area effects would still not fully explain the shift in patterns of species richness at the highest elevations.

In comparison to these spatial hypotheses, habitat-based and historical hypotheses seem to be highly relevant. The pattern of richness observed in the high elevations is driven by underlying opposing trends between long-distance and short-distance migrants. Resident species occur at relatively low frequencies and show only a slight decline that mirrors overall species richness. The seven habitat variables that showed a significant relationship with richness spanned across all three spatial scales, supporting the idea that multi-scale habitat assessment provides the optimal means for determining species-habitat relationships (Bohning-Gaese 1997, Saab 1999, Mitchell et al. 2001, Lichstein et al. 2002, MacFaden and Capen 2002). Significant microhabitat variables included a preference for proximity to water and remoteness from roads, which confirms that birds prefer to be further from human disturbance (Brotons and Herrando 2001) and closer to necessary resources. Richness also tends to increase with lower tree densities and, at least for overall and short-distance species richness, with a corresponding increase in dense, coniferous understory. In the high elevations the understory is increasingly defined by thickets of rhododendron (*Rhododendron maximum*) and mountain laurel (*Kalmia latifolia*) (Wiser et al. 1996). This may contribute to an increase in species that prefer forest-edge or open habitat, which tend to comprise more of the short-distance migrant category. In examining the two categorizations of habitat, cover type was a major correlate with richness for all migratory guilds and overall richness, in that richness tended to increase in the absence of certain cover types. While the significant cover types were unique for each guild, this highlights the closer response of richness to a more local categorization of habitat versus broad categories of habitat, which have been critizied for their ineffectiveness in predicting species presence (Cushman et al. 2008).

Two specific trends stand out in the habitat analysis at the landscape scale. First, habitat diversity is significant for all three migratory guilds. Since this variable was calculated at the point level and only includes four different habitat types, this indicates that diversity is important at the one km scale, despite the lack of overall habitat diversity throughout the region. Second, short-distance migrants show a unique pattern of positive correlation with habitat diversity and patch isolation, implying that they prefer more fragmented, isolated patches. However, all models generated from this analysis had low explanatory power ($R^2 = 0.08\text{-}0.26$) and were exclusive of elevations below approximately 1060 m (Table 2.4). It is possible that the limited elevational range used in the habitat analysis was inadequate to capture the potentially shifting influence of habitat across the gradient. Also, all habitat variables were measured exclusively at the scale of the point, which may limit ability to detect large-scale trends at the landscape level and beyond.

A different pattern emerges when looking at the habitat analysis above 1300 m where there is a divergence between long- and short-distance migrants (Table 2.5). Very few variables are retained in any model, with the exception of cover type. This is most evident for short-distance migrants, which show a significant negative relationship with several cover types, mostly the dominant forest types. This relationship, along with the overall habitat analysis, suggests that short-distance migrants prefer the more fragmented and isolated non-forested patches present only at the highest elevations in the region, and that this may be driving the increase of short-distance migrants at high elevations. The high explanatory power ($R^2_{adj} = 0.53$) supports the significance of this. In contrast, long-distance migrants retain no significant variables beyond elevation. This leaves the question, then, of what force is driving migrant richness to change in the highest elevations if habitat influences do not exist.

I suggest that historical and large-scale biogeographical factors are contributing to determining the patterns of species richness. Comparable habitat in more northern latitudes provides breeding habitat for several species of long-distance migrants which were not detected in the region we surveyed or other remnant southern forests (Rabenold 1978, DeGraaf 1991). In one study comparing bird communities of the Great Smokey Mountains National Park versus those in comparable forests in Maine, Rabenold (1978) found that two-thirds of all long-distance migrants detected were only in Maine, while only half of all short-distance migrants detected were only in Maine. Other studies in comparable northern habitats have also shown records of long-distance migrants that were not detected in this study such as Philadelphia Vireo (*Vireo philadelphicus*) and Olive-sided Flycatcher (*Contopus cooperi*) (Holmes and Sherry 2001, Faccio 2003).

These findings indicate that historically, these populations probably inhabited the southern remnants of similar northern habitat, but long-distant migrant populations were unable to persist into the present day. The decline in long-distance migrants at higher elevations is therefore due to the lack of species which we would expect to be present in high elevation breeding habitat, but whose populations have gone extinct locally. The greater habitat specialization of long-distance migrants compounds these large-scale biogeographic effects, and there is still a detectable influence of historical deglaciation in eastern North America affecting current biodiversity patterns (Hawkins and Porter 2003). This is in contrast to short-distance migrants, which consist of more species that are generalists (Poole 2005) less sensitive to fragmentation and edge habitat (Flather and Sauer 1996). The persistence of short-distance versus long-distance migrants may ultimately be rooted in differences in life history strategies, such as arrival time at breeding grounds or number of clutches.

In addition to varying patterns of species richness, the presence of 12 special status species in the study region underscores the necessity of understanding population dynamics for this region. All species, with the exception of Cerulean Warblers, had mean elevations centered in the high elevations, and all species detected more than five times showed great variation in the range of elevations at which they were found and no preference for any specific elevational band. Such widespread ranges suggest that these species would be able to adapt if there were a loss of part of their elevational range; however, analysis from Chapter 1 shows that four of these species are elevation sensitive and mostly respond to habitat beyond the microhabitat scale, so that any habitat disturbance at the landscape scale or larger could impact these populations. More intensive studies of those special status species that are not elevation sensitive or detected very rarely would indicate whether they respond to the larger landscape in a similar manner.

In summary, the observed decline in species richness across the elevational gradient is not consistent among migratory guilds, particularly at the highest elevations within the study region. Landscape fragmentation may be influencing short- and long-distance migrants at both a smaller scale of habitat type and a larger biogeographic scale. The long-term persistence of long-distance migrants may be questionable as high elevation forests become more tenuous in their own persistence: increasing global temperatures have already been linked to greater habitat fragmentation and range retraction of certain forest habitats (Thomas et al. 2006, Beckage et al. 2008). Given that these consequences in the Southern Appalachians have historically led to the disappearance of several long-distance migrants, continued climate change could result in the eventual extirpation of several more species of long-distance migrants, which would reduce overall species richness of the region. As the group of species most sensitive to elevation and habitat fragmentation, long-distance migrants are the most vulnerable group in the region due to potential landscape level changes in both composition and pattern. Conservation and management work in this region would benefit from focus on preserving existing unique habitat and monitoring the presence and distribution of species according to their migratory guilds to track changes in population trends.

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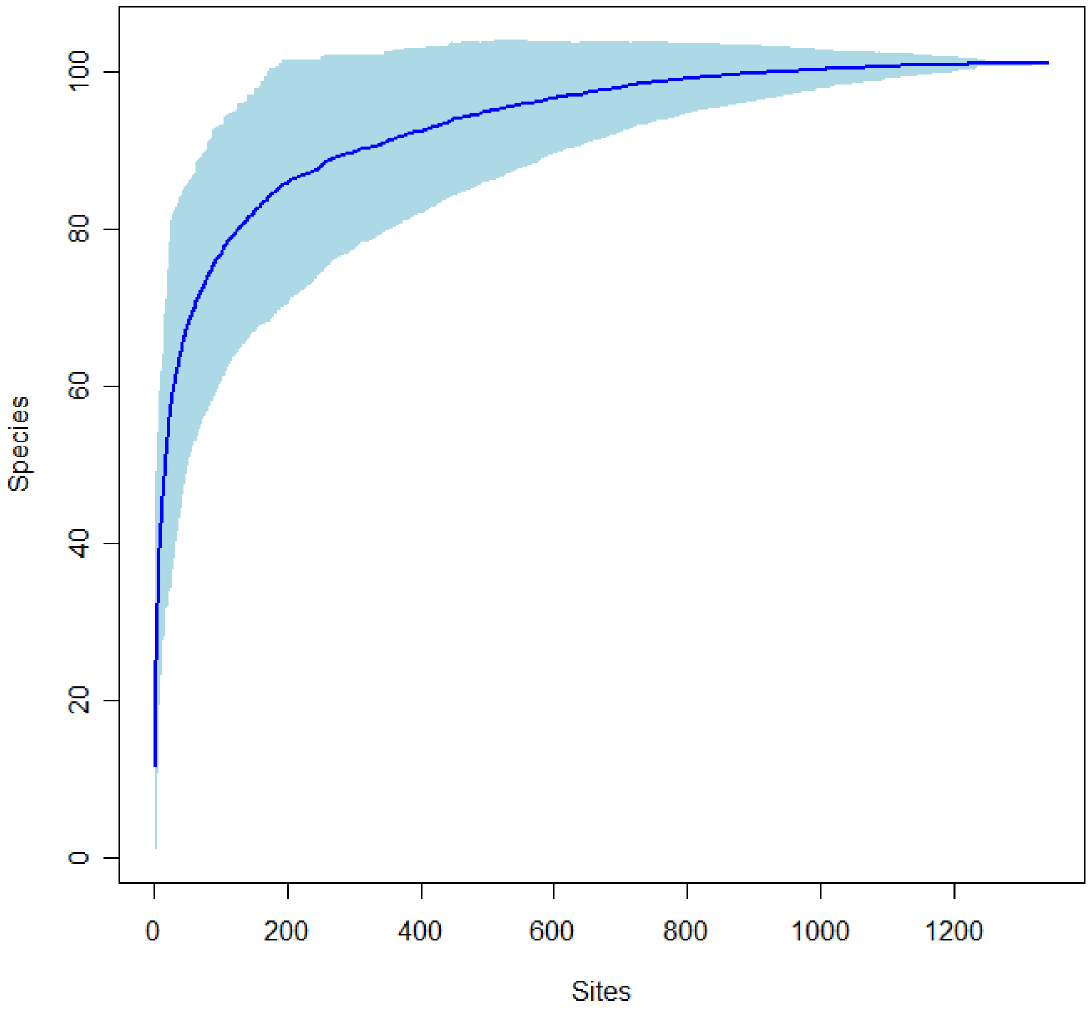

Figure 2.1. Species accumulation curve with confidence intervals. All points were randomly subsampled without replacement.

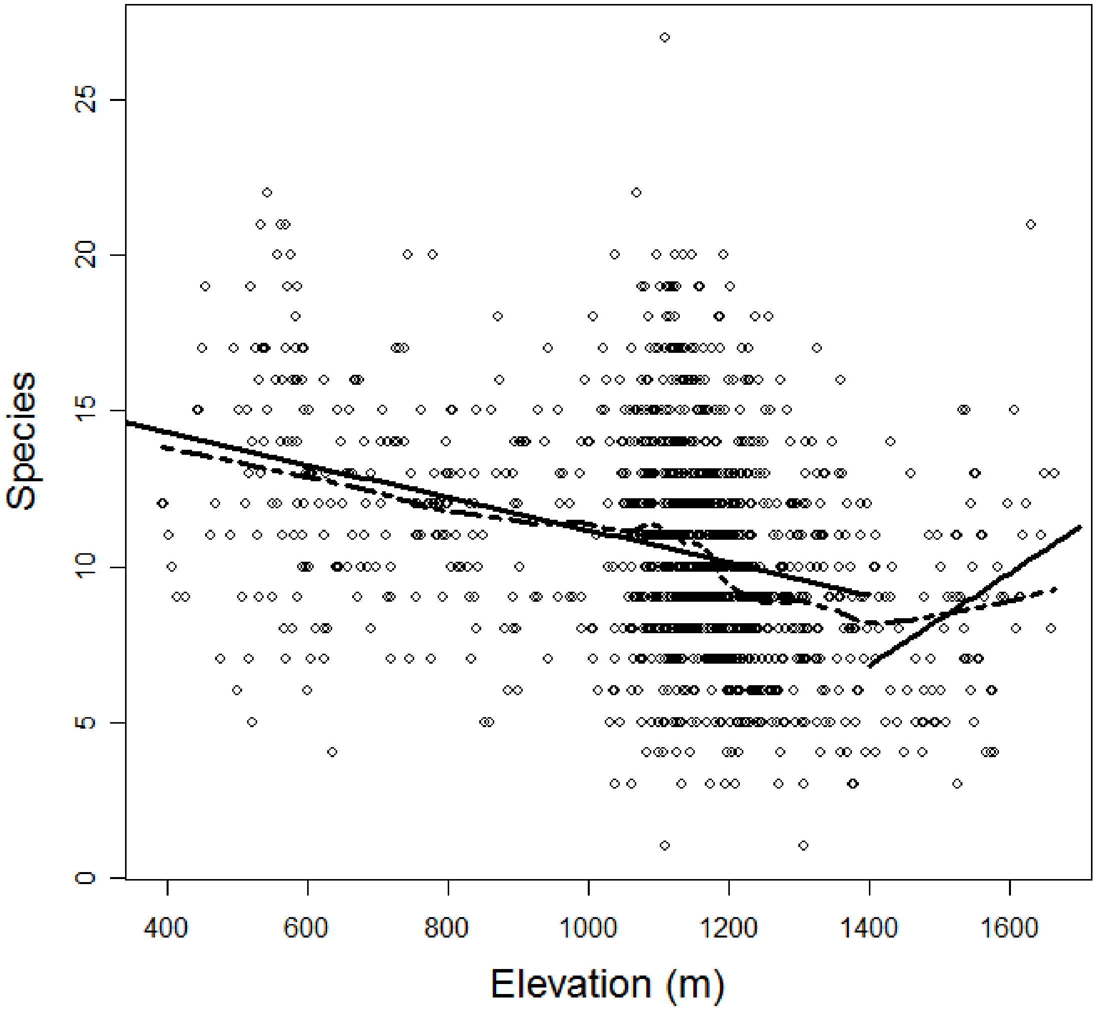

Figure 2.2. Observed species richness of all species (101). Dashed line represents a smoothing function that was calculated to determine the average richness at every value of elevation using a span of 0.3. The span value indicates the proportion of points in the plot which influence the smooth at each value, with higher span values leading to more smoothness. Solid lines represent generalized linear models that were calculated for points < 1400 m and points ≥ 1400 m.

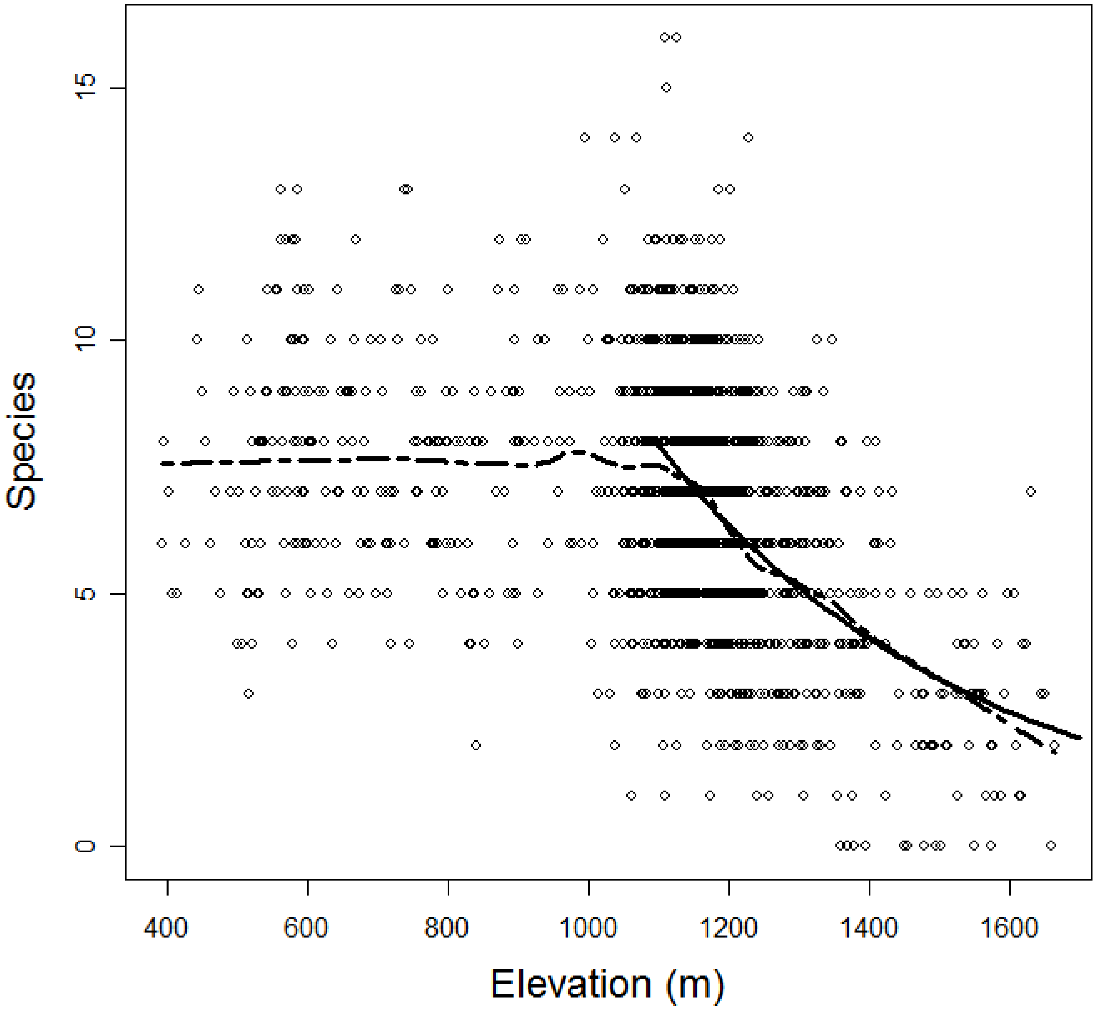

Figure 2.3. Observed species richness of long-distance migrants (49). Dashed line represents smoothing function and solid line represents generalized linear model that was calculated for points ≥ 1100 m.

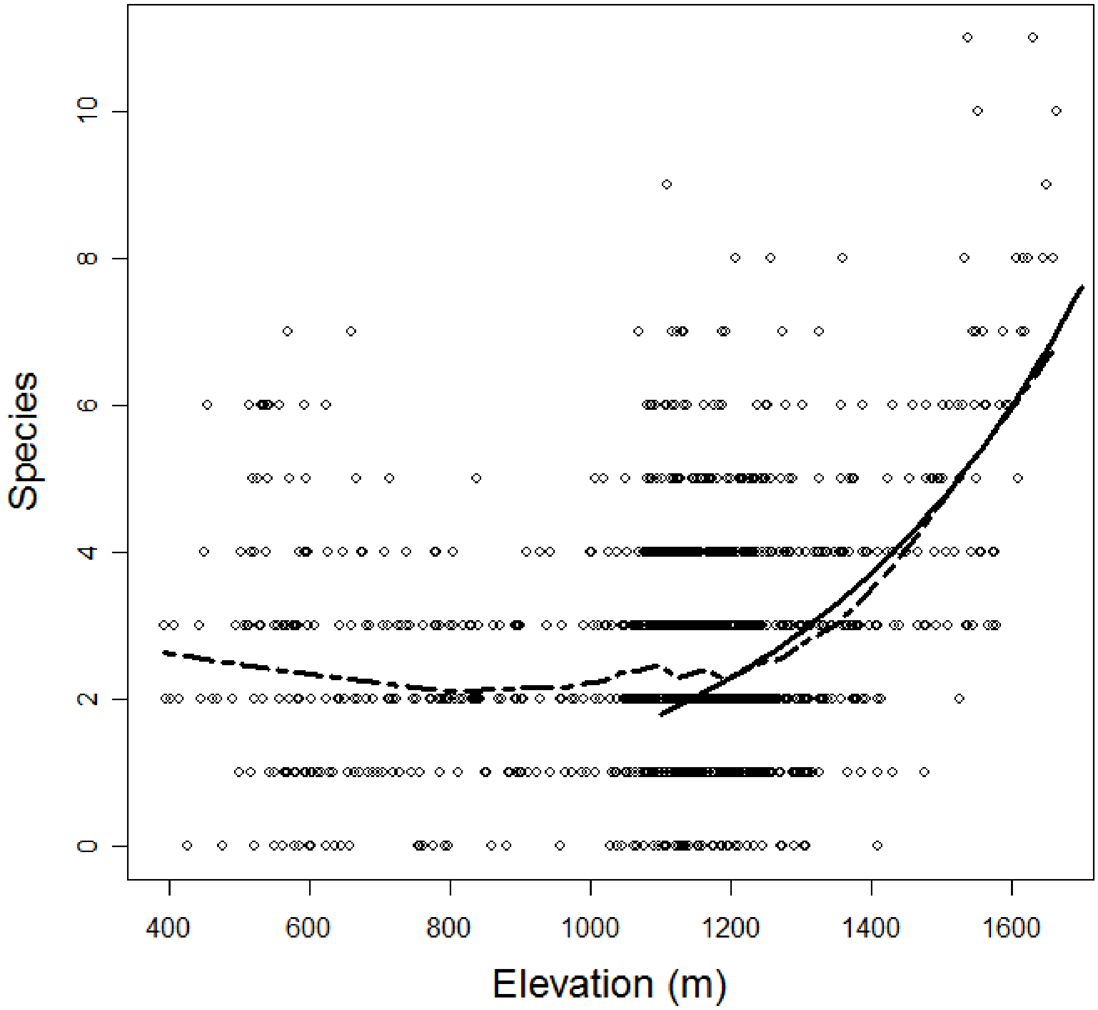

Figure 2.4. Observed species richness of short-distance migrants (35). Dashed line represents smoothing function and solid line represents generalized linear model that was calculated for points ≥ 1100 m.

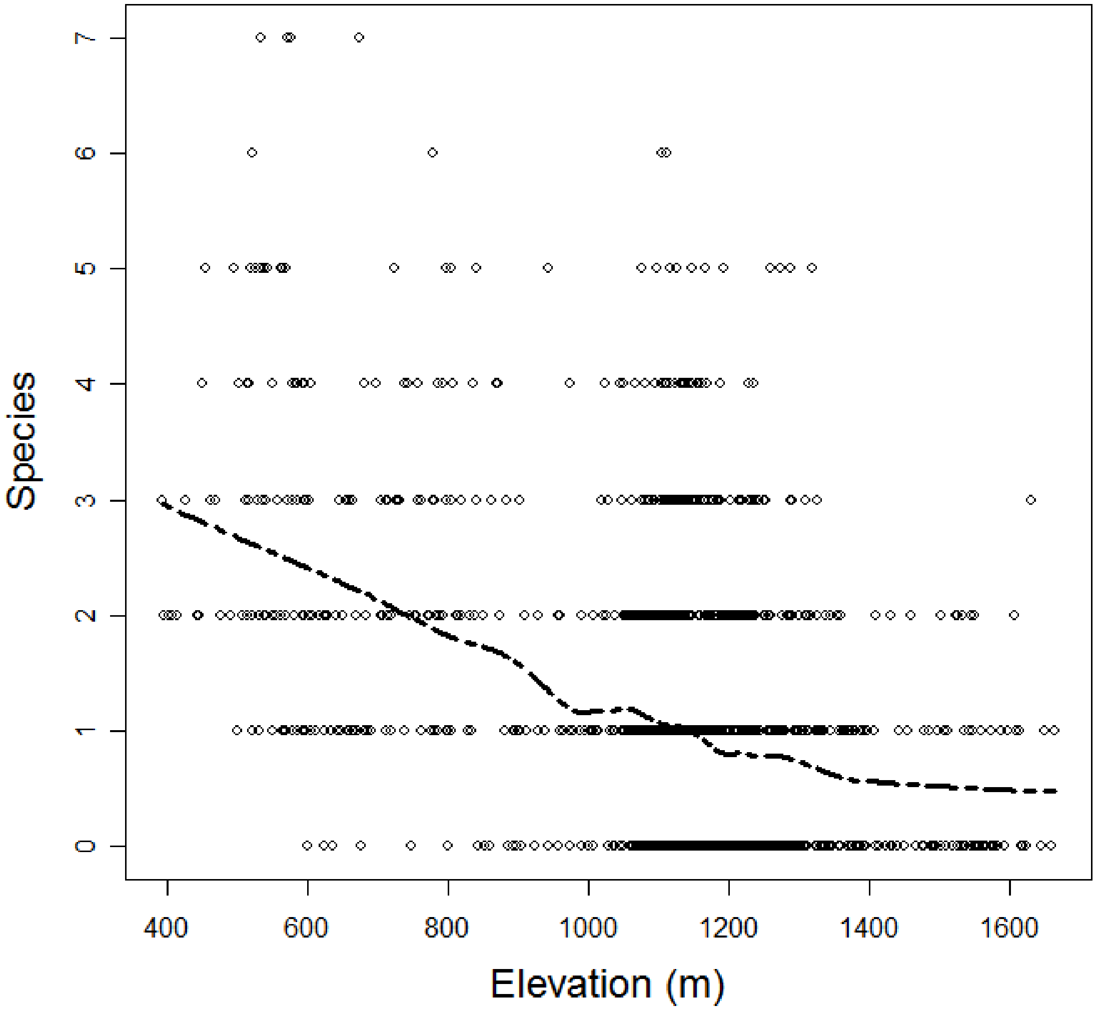

Figure 2.5. Observed species richness of residents (17). Dashed line represents smoothing function.

Table 2.1. Habitat variables used in analysis.

Scale of analysis	**Variable**	**Description**
Micro	aspect	transformed between 0 and 2 (2 = northeast, 0 = southwest)
	slope	degrees
	waterDist	distance to water, 1 = 0-25m, 2 = 25-50m, 3 = >50m
	roadDist	distance to forest edge 1 = 0-25m, 2 = 25-50m, 3 = >50m
	edgeDist	distance to public road, 1 = 0-25m, 2 = 25-50m, 3 = >50m
	canopyClass	% canopy coverage, 1 = 0-25, 2 = 25-50, 3 = 50-75, 4 = 75-100
	domGround	dominant ground cover, H = herb, L = leaves, R = rock, M = moss/lichen, W = wood
	totalTreeS	total number of tree species
	totalTreeN	total number of trees
	totalShrubS	total number of shrub species
	totalShrubN	total number of shrubs
	shrub1SConifer	presence/absence of understory dominated by evergreens
	HW	% hardwood based on ratio of conifer to deciduous diameter of top 3 tree species
Habitat	habType	1 of 4 classifications based on SEGAP data (see text)
	coverType	1 of 18 classifications based on VDGIF protocol (see text)
Landscape	habArea	area (ha) of habitat patch in which point is located
	habDiv	number of different habitat types within 1 km of point (0-4)
	habProx	fragmentation index using Proximity function in FRAGSTATS, 1 km radius
	habENN	distance to next nearest habitat patch of same type
	patchArea	area (ha) of land above threshold elevation within 1 km of point
	patchENN	distance to next nearest patch above threshold elevation

Table 2.2. All species (101) detected during the 2005-2007 breeding seasons at 1,341 points. Migratory status is (L) for long-distance migrant, (S) for short-distance migrant and (R) for resident (based on classification scheme of Gough et al. 1998).

Species	Scientific Name	Observations	Points	Migratory Status
Acadian Flycatcher	*Empidonax virescens*	281	161	L
Alder Flycatcher	*Empidonax alnorum*	2	2	L
American Crow	*Corvus brachyrhynchos*	820	494	S
American Goldfinch	*Carduelis tristis*	276	203	S
American Redstart	*Setophaga ruticilla*	413	248	L
American Robin	*Turdus migratorius*	335	199	S
Bald Eagle	*Haliaeetus leucocephalus*	2	1	S
Baltimore Oriole	*Icterus galbula*	2	2	L
Barn Swallow	*Hirundo rustica*	3	1	L
Barred Owl	*Strix varia*	24	21	R
Black-and-white Warbler	*Mniotilta varia*	951	608	L
Black-billed Cuckoo	*Coccyzus erythropthalmus*	59	50	L
Blackburnian Warbler	*Dendroica fusca*	56	37	L
Black-capped Chickadee	*Poecile atricapillus*	395	239	R
Black-throated Blue Warbler	*Dendroica caerulescens*	527	301	L
Black-throated Green Warbler	*Dendroica virens*	1112	521	L
Blue Jay	*Cyanocitta cristata*	620	453	S
Blue-gray Gnatcatcher	*Polioptila caerulea*	146	114	L
Blue-headed Vireo	*Vireo solitarius*	1114	691	L
Blue-winged Warbler	*Vermivora pinus*	2	2	L
Broad-winged Hawk	*Buteo platypterus*	19	17	L
Brown Creeper	*Certhia americana*	22	19	S
Brown Thrasher	*Toxostoma rufum*	10	9	S
Brown-headed Cowbird	*Molothrus ater*	94	65	S
Canada Warbler	*Wilsonia canadensis*	355	196	L
Carolina Chickadee	*Poecile carolinensis*	54	49	R
Carolina Wren	*Thryothorus ludovicianus*	71	59	R
Cedar Waxwing	*Bombycilla cedrorum*	193	94	S
Cerulean Warbler	*Dendroica cerulea*	13	10	L
Chestnut-sided Warbler	*Dendroica pensylvanica*	826	337	L
Chimney Swift	*Chaetura pelagica*	43	30	L
Chipping Sparrow	*Spizella passerina*	83	43	L
Common Grackle	*Quiscalus quiscula*	6	4	S
Common Raven	*Corvus corax*	264	179	R
Common Yellowthroat	*Geothlypis trichas*	21	17	L
Dark-eyed Junco	*Junco hyemalis*	2032	866	S
Downy Woodpecker	*Picoides pubescens*	169	156	R
Eastern Bluebird	*Sialia sialis*	6	6	S
Eastern Meadowlark	*Sturnella magna*	1	1	S
Eastern Phoebe	*Sayornis phoebe*	51	40	S
Eastern Screech Owl	*Megascops asio*	3	3	R
Eastern Towhee	*Pipilo erythrophthalmus*	1674	723	S
Eastern Tufted Titmouse	*Baeolophus bicolor*	564	402	R
Eastern Wood Pewee	*Contopus virens*	757	496	L
Field Sparrow	*Spizella pusilla*	138	58	S

Table 2.2. con't.

Species	Scientific Name	Observations	Points	Migratory Status
Golden-crowned Kinglet	*Regulus satrapa*	132	53	S
Gray Catbird	*Dumetella carolinensis*	150	111	L
Great Crested Flycatcher	*Myiarchus crinitus*	281	191	L
Hairy Woodpecker	*Picoides villosus*	246	204	R
Hermit Thrush	*Catharus guttatus*	86	61	S
Hooded Warbler	*Wilsonia citrina*	411	265	L
Horned Lark	*Eremophila alpestris*	1	1	S
House Wren	*Troglodytes aedon*	18	10	L
Indigo Bunting	*Passerina cyanea*	768	427	L
Kentucky Warbler	*Oporornis formosus*	12	12	L
Killdeer	*Charadrius vociferus*	1	1	S
Least Flycatcher	*Empidonax minimus*	148	58	L
Louisiana Warbler	*Seiurus motacilla*	39	29	L
Magnolia Warbler	*Dendroica magnolia*	124	77	L
Mourning Dove	*Zenaida macroura*	222	171	S
Mourning Warbler	*Oporornis philadelphia*	7	4	L
Northern Bobwhite	*Colinus virginianus*	18	12	R
Northern Cardinal	*Cardinalis cardinalis*	94	77	R
Northern Flicker	*Colaptes auratus*	174	154	S
Northern Mockingbird	*Mimus polyglottos*	4	4	R
Northern Parula	*Parula americana*	51	43	L
Ovenbird	*Seiurus aurocapilla*	2972	1183	L
Peregrine Falcon	*Falco peregrinus*	5	4	L
Pileated Woodpecker	*Dryocopus pileatus*	451	351	R
Pine Siskin	*Carduelis pinus*	1	1	S
Pine Warbler	*Dendroica pinus*	115	87	S
Prairie Warbler	*Dendroica discolor*	8	8	L
Purple Finch	*Carpodacus purpureus*	2	2	S
Red-bellied Woodpecker	*Melanerpes carolinus*	69	63	R
Red-breasted Nuthatch	*Sitta canadensis*	107	70	S
Red-eyed Vireo	*Vireo olivaceus*	3532	1328	L
Red-shouldered Hawk	*Buteo lineatus*	9	9	S
Red-tailed Hawk	*Buteo jamaicensis*	18	12	S
Red-winged Blackbird	*Agelaius phoeniceus*	6	3	S
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	544	346	L
Ruby-throated Hummingbird	*Archilochus colubris*	33	33	L
Ruffed Grouse	*Bonasa umbellus*	69	58	R
Scarlet Tanager	*Piranga olivacea*	1459	920	L
Sharp-shinned Hawk	*Accipiter striatus*	1	1	S
Song Sparrow	*Melospiza melodia*	26	19	S
Swainson's Thrush	*Catharus ustulatus*	2	2	L
Swainson's Warbler	*Limnothlypis swainsonii*	17	11	L
Tree Swallow	*Tachycineta bicolor*	22	4	S
Veery	*Catharus fuscescens*	1405	608	L
Whip-poor-will	*Caprimulgus vociferus*	3	3	L
White-breasted Nuthatch	*Sitta carolinensis*	355	288	R

Table 2.2. con't.

Species	Scientific Name	Observations	Points	Migratory Status
White-eyed Vireo	*Vireo griseus*	6	6	L
Wild Turkey	*Meleagris gallopavo*	37	32	R
Winter Wren	*Troglodytes troglodytes*	75	53	S
Wood Thrush	*Hylocichla mustelina*	567	400	L
Worm-eating Warbler	*Helmitheros vermivorum*	485	299	L
Yellow-bellied Sapsucker	*Sphyrapicus varius*	93	65	S
Yellow-billed Cuckoo	*Coccyzus americanus*	295	223	L
Yellow-breasted Chat	*Icteria virens*	22	13	L
Yellow-rumped Warbler	*Dendroica coronata*	75	48	S
Yellow-throated Vireo	*Vireo flavifrons*	5	5	L

Table 2.3. Elevational ranges of detected species that are listed as special status by the Virginia Department of Game and Inland Fisheries (VDGIF 2006).

Species	# Observations	Min Elev (m)	Max Elev (m)	Mean Elev (m)	Range (m)
Alder Flycatcher	2	652	1631	1142	979
Bald Eagle	1	1132	NA	1132	NA
Brown Creeper	19	1089	1631	1329	542
Cerulean Warbler	7	393	1167	723	774
Golden-crowned Kinglet	53	1050	1661	1418	611
Hermit Thrush	61	1118	1666	1403	548
Magnolia Warbler	77	644	1625	1219	981
Mourning Warbler	4	1126	1238	1192	112
Peregrine Falcon	4	1082	1155	1124	73
Purple Finch	2	1608	1666	1637	58
Red-breasted Nuthatch	69	839	1652	1396	813
Winter Wren	53	893	1631	1358	738

Table 2.4. Habitat analysis of species richness of all species, long-distance migrants, short-distance migrants and resident species in all elevations over approximately 1070 m. A (+) or (-) indicates the direction of the relationship and number of (+) or (-) represents the p-value (+ < 0.05, ++ < 0.01, +++ < 0.001). Categories for cover type that are significant are as follows: All (laurel thicket, open), Long-distance (laurel thicket), Short-distance (cove hardwoods, chestnut oak, hemlock, maple, mixed oak, northern red oak, pine, uplands hardwood), Residents (spruce/fir).

	Microhabitat variables													**Habitat vars**		**Landscape variables**					R^2_{adj}
Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**	**Q**	**R**	**S**	**T**	
All			++	---					--		+++			--					++	---	0.13
Long-distance			+	---					--					---			--			---	0.25
Short-distance				---				-			+++			--			+++		+++	+++	0.26
Residents			+						-			-		-			---			-	0.08

Micro
A aspect
B slope
C waterDist
D roadDist
E edgeDist
F canopyClass
G domGround
H totalTreeS
I totalTreeN
J HW
K shrub1SConifer
L totalShrubS
M totalShrubN

Habitat
N coverType
O habType

Landscape
P habArea
Q habDiv1km
R habProx1km
S habENN

T elevation

Table 2.5. Habitat analysis of species richness of all species, long-distance migrants, short-distance migrants and resident species in high elevations only (over 1300 m). A (+) or (-) indicates the direction of the relationship and number of (+) or (-) represents the p-value (+ < 0.05, ++ < 0.01, +++ < 0.001). Categories for cover type that are significant are as follows: All (maple, northern hardwood, northern red oak), Short-distance (cove hardwood, maple, northern hardwood, northern red oak, upland hardwood), Residents (spruce/fir).

	Microhabitat variables													**Habitat vars**		**Landscape variables**					R^2_{adj}
Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**	**H**	**I**	**J**	**K**	**L**	**M**	**N**	**O**	**P**	**Q**	**R**	**S**	**T**	
All				-										-			-				0.26
Long-distance																				**--**	0.37
Short-distance														--						**+**	0.53
Residents														-			-				0.01

Micro
A aspect
B slope
C waterDist
D roadDist
E edgeDist
F canopyClass
G domGround
H totalTreeS
I totalTreeN
J HW
K shrub1SConifer
L totalShrubS
M totalShrubN

Habitat
N coverType
O habType

Landscape
P habArea
Q habDiv1km
R habProx1km
S habENN

T elevation